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Fisheries Research Bulletin No. 13

A Study on Age, Growth, and Population Structure of the Snapper, *Chrysophrys auratus* (Forster), in the Hauraki Gulf, New Zealand

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by
L. J. Paul

Fisheries Research Division
New Zealand Ministry of Agriculture and Fisheries

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[National Publicity Studios photo.

Frontispiece: A snapper catch being unloaded at the port of Auckland.

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FOREWORD

SINCE the country was first settled the snapper has been the most important food fish in New Zealand and the Hauraki Gulf the principal source of supply. The Gulf, which is fairly circumscribed, nevertheless offers a wide variety of habitats, most of which the fish are able to exploit.

Mr Paul, who has studied the fish and the fishery for the past 13 years, has collected a wealth of data, often using limited facilities. He has drawn on some of the data and on his experience in preparing this bulletin, which deals primarily with the biology of the fish. This information is an essential prerequisite for effective management of the fishery, which even now may be close to being overexploited.

Several of the factors which influence the capacity of the stock or stocks to sustain the present heavy fishing pressure are discussed, and attention is drawn to others on which further information is required if best use is to be made of this valuable resource.

G. DUNCAN WAUGH,
Director, Fisheries Research Division

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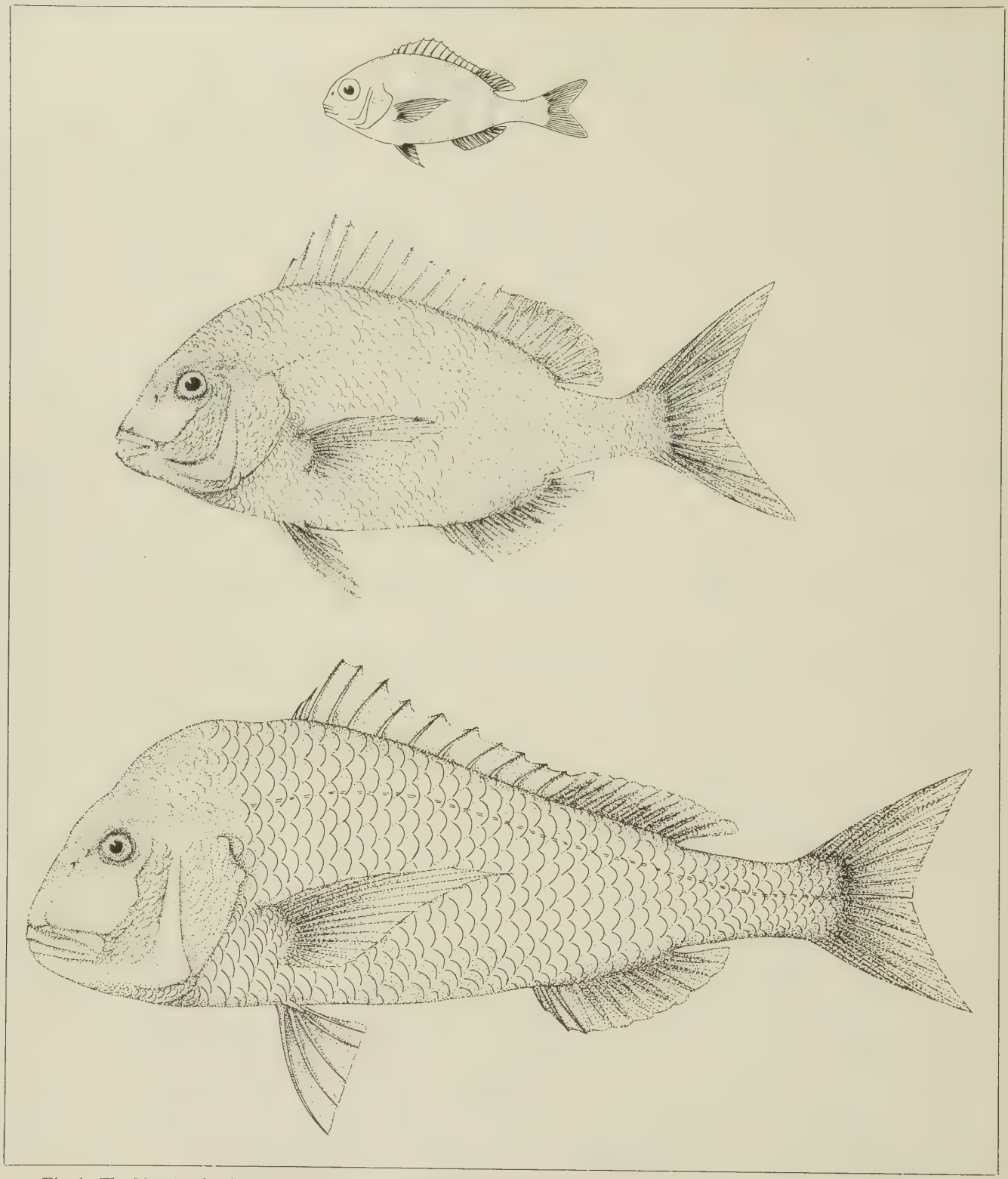

Fig. 1: The New Zealand snapper, *Chrysophrys auratus* (Forster, 1801). Top: 0-year juvenile about 3 months old, about 4 cm long. Middle: Small adult 6–10 years old, about 30 cm long. Bottom: Large adult over 25 years old, about 75 cm long. Each drawing has been generalised from several specimens, and the three do not conform to a common scale.

INTRODUCTION

The snapper, *Chrysophrys auratus* (Forster, 1801), is one of New Zealand's most common and important marine fishes (Fig. 1). It supports a valuable commercial fishery in the north of the North Island (Paul 1974, in press) and ranks high as a light-tackle game fish throughout its range. It has usually taken first place in the commercial fin fish landings for both weight landed and total value. During the period 1945–71 it contributed about 30% by weight and 25% by value to the total marine fish catch.

At least half of the New Zealand snapper catch is landed into the port of Auckland, and most of it is taken from the Hauraki Gulf fishing grounds. Boats from Thames, Coromandel, and Whangarei land small quantities. The annual catch from these grounds has steadily increased since 1953, and because of the fishery's importance there is an obvious need for information on the biology of snapper to ensure a continuing rational exploitation of the stock. Studies on the available catch and effort data for this fishery are presented elsewhere (Paul 1974, in press).

The work of Cassie (1956c) and Longhurst (1958) on age and growth rested on the assumption that scale growth rings (annuli) were formed annually. The present study sought to confirm this and thereby establish a reliable ageing technique which could be used to determine seasonal, annual, and regional variations in growth rate and age composition and to detect fluctuations in year class strength of Hauraki Gulf snapper.

Snapper occupy a variety of habitats, and some are known to move considerable distances. Early in this study it became apparent that the fish regarded as "Gulf snapper" showed a range of growth rates, and that the length-frequency distributions of Gulf snapper "populations" showed variation with both space (different habitats) and time (different years). Consequently the study was directed towards exploring this variability, with the objective of establishing both a generalised relationship between age, size, and weight in snapper and some indication of the nature and extent of such regional and temporal variations.

In the face of such variability, and with the inherent problems in sampling fish populations from trawl catches, certain assumptions on which to base the analyses of growth rate and age structure had to be retained or made. These are stated in the appropriate sections of the text.

NOMENCLATURE

The New Zealand snapper, *Chrysophrys auratus*, belongs to the sea bream family, Sparidae. The name "snapper" results from an early confusion with the true snappers (family Lutjanidae), but is in such general usage that any change is now unlikely.

Chrysophrys auratus is very similar to the Australian snappers *C. unicolor* Quoy and Gaimard, 1824, and *C. guttulatus* Valenciennes, 1830. Akazaki (1962) unites them as *Pagrus auratus* and lists as their closest relative the Japanese red sea bream, *Pagrus major* (Temminck and Schlegel, 1842). However, the name *Pagrus* has not been accepted by many subsequent Japanese workers, and the relationships of the Australasian forms to each other and to the Japanese species are still uncertain. The established name *Chrysophrys auratus* has therefore been retained in this bulletin. The specific authority usually cited is Forster, 1801, occasionally Forster *in* Bloch and Schneider, 1801; Forster's manuscript containing the original description is quoted at length in Bloch and Schneider's 1801 book.

The Maori name "tamure" is rarely used, and "snapper" is the only common name for this species throughout New Zealand. The term "bream" or "brim" is applied by fishermen to small (20–30 cm) snapper in some localities, and slightly larger, brightly coloured fish caught during the spawning season are called "school snapper"; in both these terms there is an implication that these fish represent distinct "classes", or life history stages, of snapper.

PREVIOUS WORK

There are numerous minor references to snapper in books, ships' journals, and papers from 1769 (Captain James Cook's visit) onwards. Few are relevant to this bulletin, being check lists or containing only brief notes on description, distribution, and feeding habits. Graham (1953) gave the first general account of the snapper's life history.

The more significant papers relating to the Hauraki Gulf snapper and its fishery are those of Hefford (1929), Cassie (1955–60), Longhurst (1958), Paul (1967, 1968a), and Godfriaux (1969).

Hefford (1929) summarised the development of the fishery and gave some preliminary observations on the snapper's biology—spawning grounds, nursery areas, and the size distribution of adult fish. At about the same time Marine Department staff investigated the spawning and feeding habits of snapper. Between 1925 and 1934 M. W. Young and C. Daniel observed the distribution of snapper eggs in the Hauraki Gulf and their fertilisation, hatching, and early larval development. Most of their records have unfortunately been lost, but brief accounts survive in the annual *Report on Fisheries* for that period (New Zealand Marine Department 1929, 1931, 1932), in Hefford (1929), and in a later paper on snapper spawning (Cassie 1956b). Feeding studies were mentioned in the annual *Report on Fisheries* for 1927–28 and 1928–29, and the complete data for 1927–31 are summarised by Powell (1937).

From 1948 onwards the Marine Department's research trawler *Ikatere* was used to collect data on snapper in the Hauraki Gulf. Cassie (1955) analysed the escape of small snapper through various sizes of trawl mesh and used many of the snapper obtained during these experiments for his studies of spawning, development of the eggs and early larvae, age and growth, and length-weight relationship (Cassie 1956a, 1956b, 1956c, 1957b).

Age and growth studies were continued by Longhurst (1958), who made the first definite statements on the growth rate of adult as well as juvenile Hauraki Gulf snapper. He considered the problem of the small average size of these fish, compared with snapper from other fishing grounds, and suggested that they might comprise a racially separate stock of slower-growing snapper.

Fishermen have long declared that they recognise two distinct classes of snapper within the Hauraki Gulf itself—"residents" and "school fish", the latter being caught only during the spawning season. This feature has not yet been properly investigated; the authors mentioned above all considered the possibility of two different populations of snapper occurring in the Hauraki Gulf area, but were unable to reach a firm conclusion.

Tagging of snapper to determine their seasonal migrations was done between 1952 and 1963, several thousand being released in the Hauraki Gulf, but relatively few were recaptured (McKenzie 1960, Allen 1963, Paul 1967).

Since 1959 extensive data have been collected on the distribution and abundance, length-frequency distribution, gonad condition, gut contents, and length-weight relationships of snapper trawled by *Ikatere* on the fishing grounds along the north-east coast of New Zealand. McKenzie (1960) made brief mention of this work, and Tong and Elder (1968) incorporated some of the data in their general assessment of the stocks of commercially important demersal fish species in the Bay of Plenty.

Observations on the seasonal cycle of water temperatures in the Hauraki Gulf in 1965–66 have been published separately (Paul 1968b). A brief study was made of early scale growth in the snapper (Paul 1968a) as related to scale-sampling procedures and accurate back calculation of fish growth. Observations on the feeding habits of Hauraki Gulf snapper have also been published (Godfriaux 1969, 1970, Colman 1972).

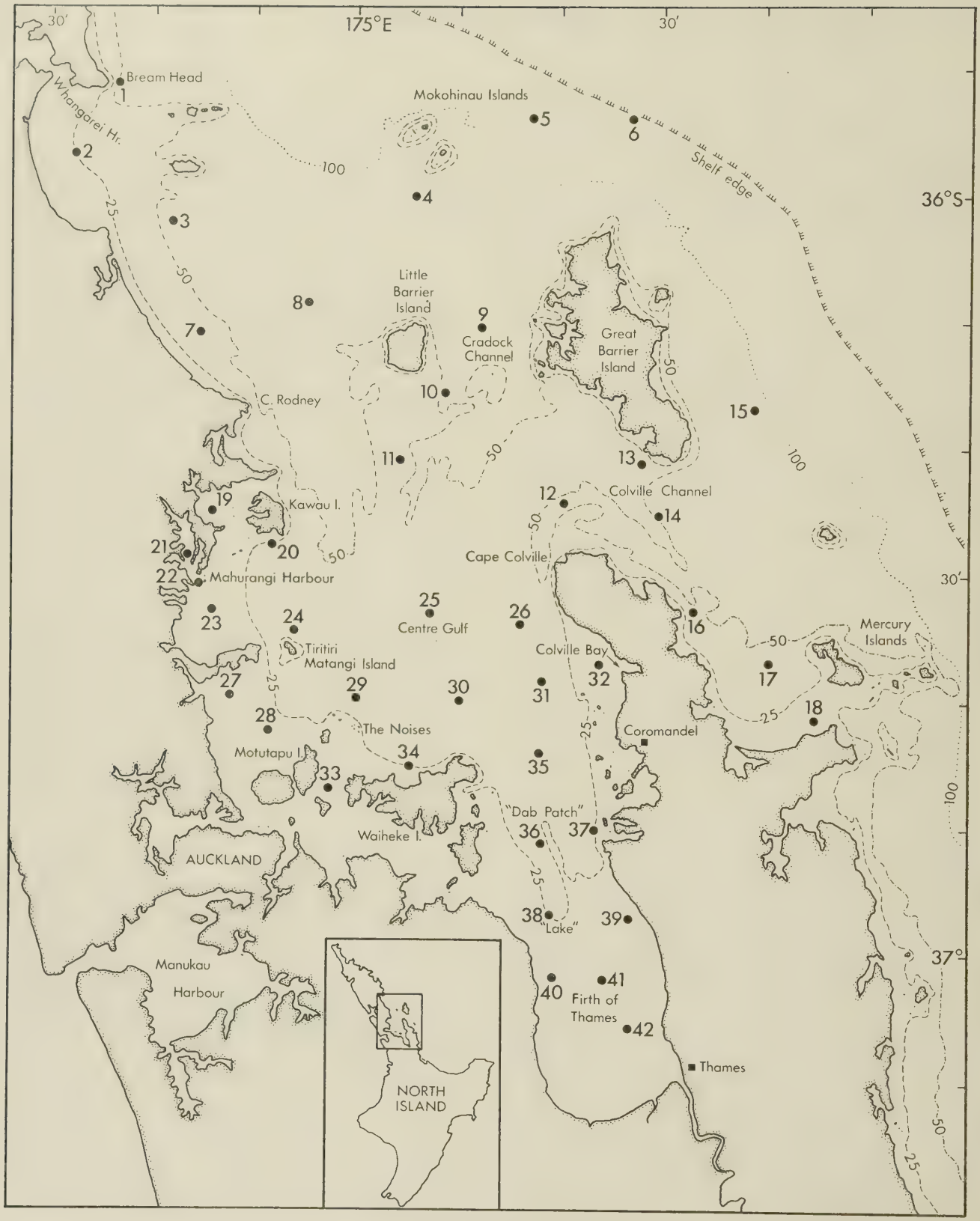

Fig. 2: Hauraki Gulf, New Zealand. Depth contours are in metres, simplified from Eade (1972). Station positions are shown by numbered solid circles; data are as in Table 1.

MATERIAL AND METHODS

STUDY AREA

The Hauraki Gulf is here defined as that area of water between Bream Head in the north-west and the Mercury Islands in the south-east (Fig. 2). It may be divided into the "inner Gulf", south of a line from Cape Rodney to Cape Colville, and the "outer Gulf", seawards of this line. If its outer boundary is taken as the 100-m contour, the Hauraki Gulf covers about 9000 km² (about 2700 square nautical miles), of which 2700 km² (800 square nautical miles) are shallow harbours and bays less than 25 m deep, 3200 km² (900 square nautical miles) are from 25 to 50 m deep, and 3400 km² (1000 square nautical miles) are 50 to 100 m deep. The shelf edge occurs at about 150 m.

TABLE 1: Trawl stations in the Hauraki Gulf, 1964–70 (positions shown in Fig. 2).

Station No.	Name	Depth (m)*	No. of samples
1	Bream Head	40–60	6
2	Bream Bay	20–25	6
3	Sail Rock	35–55	3
4	Simpsons Rock	73	1
5	North-east of Mokohinau Islands	135	1
6	North of Great Barrier Island	145–155	1
7	Pakiri Beach	55	6
8	North-west Reef	55–65	2
9	Cradock Channel	55–65	12
10	Horn Rock	45–55	7
11	South of Little Barrier Island	50	5
12	Channel Island	45–50	2
13	Tryphena	20–45	2
14	Colville Channel	45–55	3
15	East of Great Barrier Island	90	8
16	Te Anaputa	35–55	5
17	West of Mercury Islands	45–50	3
18	Te Paki	18	1
19	Kawau Bay	4–15	5
20	Kawau Island	20–40	30
21	Inner Mahurangi Harbour	4	5
22	Mahurangi Harbour Entrance	5–18	11
23	Outer Mahurangi Harbour	15–20	5
24	Tiritiri Matangi Island	25–35	10
25	Centre Gulf	45	10
26	The Quarries	40–45	1
27	Karepiro Bay	15	1
28	Toroa Point (Gull Point)	20	5
29	North of The Noises islands	25–35	4
30	Horuhoru Rock (Gannet Rock)	38	3
31	Motukawao Group	37	1
32	Colville Bay (Cabbage Bay)	15–45	15
33	Motuihe Channel, Motutapu Island	11–17	9
34	Onetangi Bay	15–25	6
35	Waiheke–Coromandel	33–42	8
36	"Dab Patch"	22–27	85
37	Deadmans Point	20–30	4
38	"Lake"	15–25	11
39	Tapu	10	3
40	Kaiaua (New Brighton)	10	5
41	Firth	5–15	13
42	Thames	4	3

* The depth was recorded in fathoms, and some rounding to 0 or 5 was done during conversion to metres, particularly when successive hauls occurred at slightly different depths. Ranges greater than 5 m are given; smaller ranges are given as a middle value.

Unpublished data indicated that there was considerable variability in the size range and abundance of snapper in different and sometimes localised areas. Therefore emphasis was placed on obtaining a large number of samples from a variety of areas rather than on detailed examination of a few large samples. To examine some specific points, however, the latter approach was necessary.

Between 1964 and 1970 snapper samples were obtained from 42 localities, ranging from shallow bays and estuaries only a few metres deep to stations near the edge of the continental shelf (Fig. 2, Table 1). This wide coverage was intended to include all known snapper habitats accessible to trawling, but most work was done in the sheltered inner Gulf.

SAMPLING

Trawling

Ikatere, a 19-m (63-ft) trawler, towed standard cotton or nylon trawl nets during the sampling period. A 2.5- or 3.8-cm (1- or 1½-in.) liner was used inside the 11.8-cm (4½-in.) cod-end. Because of damage and losses several different nets, of 18–21 m (60–70 ft) ground rope length, were used, but they were essentially similar and were considered to have similar fishing characteristics for qualitative sampling purposes.

The duration of hauls ranged from 5 minutes in the shallow areas to 2 hours in the deeper localities, most being of 20, 30, or 60 minutes. This depended partly on the size of the locality (for example, a small harbour channel allowing only a brief haul) and partly on the expected number of snapper in the catch, the intention being where possible to obtain 200 to 500 fish.

Beach Seining

A 6-m (20-ft) net with 1.3-cm (½-in.) mesh was used to collect samples from Manukau Harbour from March to July 1965 and from the south-western Hauraki Gulf harbours and bays in February and March 1966.

Commercial Snapper Catch

Several samples of Hauraki Gulf trawl-caught snapper were measured in Auckland fish sheds between March and June 1964, and regular 2-monthly samples were obtained from 1966 onwards. Some samples of

Danish seine-caught snapper were measured in 1969, 1970, and 1971.

Measurements

All fish were measured in the field as fork length, to the nearest centimetre below.

Scale and Otolith Samples

Scales were taken from a standard site on the central flank of the fish (see Paul 1968a). From 10 to 20 scales were taken from small to medium fish and more from larger fish to allow for a higher proportion of replacement scales.

The fairly large and robust otoliths were easily obtained by making a dorso-lateral cut part way through the head at the level of the pre-operculum, then breaking the skull open to expose the otic capsule. They were cleaned of adhering tissue and stored dry with the scales in serially numbered envelopes (Paul 1966).

Reproductive Condition

During the 1965–66 spawning season (November–January) several samples of snapper were sexed and the gonad development stages determined after the method of Cassie (1956b). Additional observations of fish size and gonad maturity were made during subsequent spawning seasons as opportunity permitted.

ANALYSIS

Length Measurements

The 1-cm units used for the original measurements were retained in analysis and presentation of most of the data; some of the generalised length-frequency data are grouped into 2-cm units for better comparison with some early measurements in inches. Modal values were generally determined by eye, but the method of Cassie (1950, 1954) was used for the main series of Kawau Island samples.

Scale Reading

Several scales from each fish were cleaned briefly in water, checked for general clarity of growth rings, and dry mounted between two microscope slides. The number examined varied with the scale's size, availability, and clarity; about five with clear growth rings were checked from small fish and about 10 from large fish with thick scales and obscure growth rings. Final examination and measurement were made through a stereomicroscope at magnifications between 10× and 40× with transmitted light. This method was slower than using a conventional projecting scale reader, but allowed more detailed examination of difficult scales or parts of scales. All scale measurements were made at 10× magnification from the scale's focus along an antero-lateral radius. The reasons for using the latter measurement are given in Paul (1968a).

To facilitate rapid calculation of growth rates a fish length-scale size nomograph was constructed according to the description of Hile (1950, 1970).

Otolith Reading

Two methods were used. In the first the whole otolith was immersed in cedarwood oil and viewed through a stereomicroscope at 10× to 40× magnification, in reflected light, against a dark background. Concentric arrangements of light and dark rings were clearly visible. The second method was a modification of the technique described by Christensen (1964), in which the otolith was broken in half, at right angles to the longest dimension, and the broken cross section surface polished smooth, heated slightly in a low flame, and viewed in both reflected and transmitted light. The clearest definition of the light and dark concentric rings was obtained with reflected light when the otolith section was completely immersed in cedarwood oil, but sufficient clarity for age determination was obtained by brushing a thin film of oil over the sectioned surface.

DEFINITIONS

Scales

The average snapper scale is almost rectangular, with fine circuli in the large anterior field and small ctenii bordering the short posterior field (Fig. 3). The innermost circuli are arranged concentrically around the scale's focus, but those a short distance out run from one side of the scale to the other, becoming almost linear at the scale's anterior margin. Thus they cannot represent regular growth increments as they do in some fishes. At intervals the circuli are interrupted or broken by rings running parallel to the edge of the scale; these are annuli and represent regular and significant growth checks in the fish's life history. Unfortunately, no single criterion can be used for their recognition. "Cutting-over" of 1 year's circuli by the first circulus of the following year is a widely accepted characteristic of an annulus on a ctenoid scale, but is not a constant or conspicuous feature of snapper scale annuli, particularly the first 2 or 3 annuli. However, most annuli appear distinctly dark in transmitted light, and this characteristic, with cutting-over when present, was used to distinguish true annuli from occasional minor growth interruptions. Growth zones are the scale areas between successive annuli.

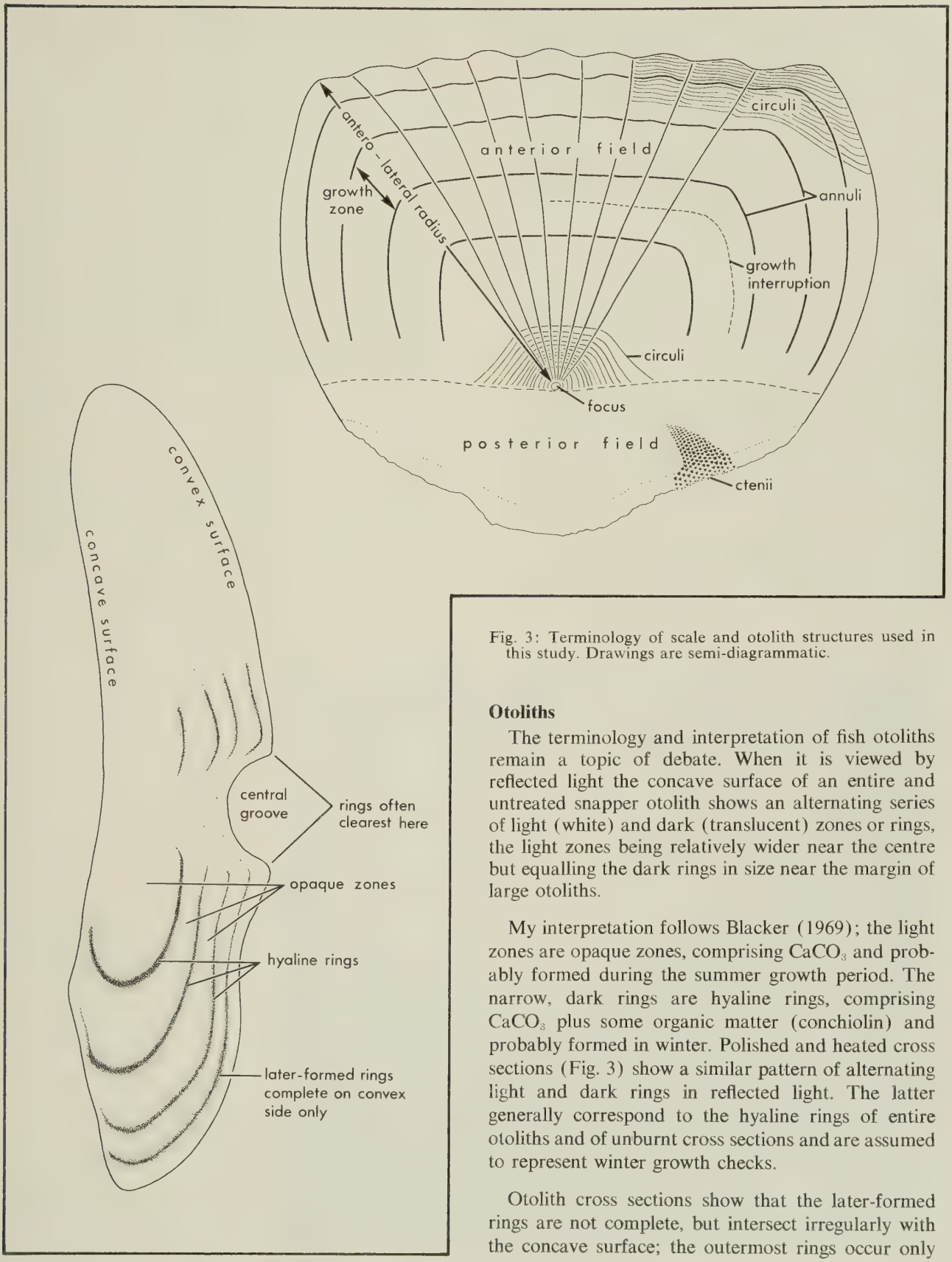

Fig. 3: Terminology of scale and otolith structures used in this study. Drawings are semi-diagrammatic.

Otoliths

The terminology and interpretation of fish otoliths remain a topic of debate. When it is viewed by reflected light the concave surface of an entire and untreated snapper otolith shows an alternating series of light (white) and dark (translucent) zones or rings, the light zones being relatively wider near the centre but equalling the dark rings in size near the margin of large otoliths.

My interpretation follows Blacker (1969); the light zones are opaque zones, comprising $CaCO_3$ and probably formed during the summer growth period. The narrow, dark rings are hyaline rings, comprising $CaCO_3$ plus some organic matter (conchiolin) and probably formed in winter. Polished and heated cross sections (Fig. 3) show a similar pattern of alternating light and dark rings in reflected light. The latter generally correspond to the hyaline rings of entire otoliths and of unburnt cross sections and are assumed to represent winter growth checks.

Otolith cross sections show that the later-formed rings are not complete, but intersect irregularly with the concave surface; the outermost rings occur only

as thin layers of alternating hyaline and opaque material deposited over the convex surface. Consequently rings were counted from the centre out to this surface; usually they were most clearly differentiated on either side of the large central groove.

Year Classes and Age Groups

Cassie (1956b) found that snapper spawn during spring and summer, October to March. During this study fish with ripe gonads were found during these months and "running ripe" fish from November to February. The reproductive cycle of snapper is inadequately known, and it is not clear whether (a) individual fish spawn regularly but intermittently from October to March, (b) individuals have staggered, discrete spawning times, some spawning each month from October to March, or (c) different populations spawn at different, restricted periods. Nevertheless, for the purposes of this study 1 January can be assigned as the theoretical birthday (Longhurst 1958), so that the calendar year represents 1 year of growth. Thus during its first year, from 1 January to 31 December, a snapper will be in the 0+ age group. And it is assigned to the year class of its first year; for example, fish spawned between October 1964 and March 1965 are assigned to the 1965 year class.

Maturity: Juveniles and Adults

The breeding cycle of snapper was not studied in detail, and a somewhat arbitrary distinction had to be made between "juveniles" and "adults" to allow compilation of age, growth, and distribution data. Almost all fish less than 20 cm in length had undeveloped gonads and were regarded as juveniles. Most fish between 20 and 24 cm had small but ripe gonads during the breeding season, and virtually all fish 25 cm and over had obviously ripe and running ripe gonads; the contribution of the former group to the spawning stock is uncertain, and though they might represent maturing but non-spawning "adolescents", for most practical purposes they can be included with the larger fish as adults and are discussed as such in this bulletin.

Seasons

Hydrologically summer is January to March, autumn April to June, winter July to September, and spring October to December (Paul 1968b), and these groupings of months were made to simplify discussion of data.

AGE AND GROWTH

Several accounts of the age and growth of snapper have already appeared (Cassie 1955, 1956c, Longhurst 1958, McKenzie 1960), principally based on scale reading. Cassie (1956c) found scale reading to be rather unreliable for Hauraki Gulf fish (though he suggested that scales of snapper from other geographical areas, for example, Tasman Bay, might be more suitable) and recommended that length-frequency analysis of samples of small fish should be carried out in conjunction with scale reading. Longhurst (1958) had insufficient material for this and had to use age at capture, determined by scale reading alone, for his estimates of growth rates. McKenzie (1960) assembled all available data from scale reading and length-frequency analyses to show the average growth rate for the snapper's first 5 years of life.

However, few of the fundamental observations on which scale reading must depend were made by these workers, and subsequent study has shown that scales taken from above the lateral line (used by them) are unsuitable for ageing larger fish (see page 38 and Paul 1968a). The annual nature of scale ring formation was assumed. Cassie (1956c) stated that the annulus was apparently formed at the time of spawning, which occurs between October and March; this was also accepted by Longhurst (1958). The suggestion that the adult annuli denoted spawning checks, rather than a winter cessation of growth, raised the problem of what the annuli on the scales of immature fish really represented. Annulus formation in most fishes is annual (Van Oosten 1929, Berg and Grimaldi 1967), but this cannot be assumed. Shindo (1960) found a complex relationship between number of annuli and age in the yellow sea bream *Taius tumifrons*. The annual nature of annulus formation in the snapper had to be more firmly established before routine scale reading for age and growth was done.

It seemed appropriate to follow Cassie's (1956c) suggestion that the growth rate of young snapper should be determined by length-frequency analysis of regular samples from the same locality. Scale annulus formation could then be followed on groups of fish of known age.

An examination of existing snapper length-frequency data showed that large numbers of small snapper were regularly caught at a locality just south of Kawau Island in the inner Gulf and that they formed several

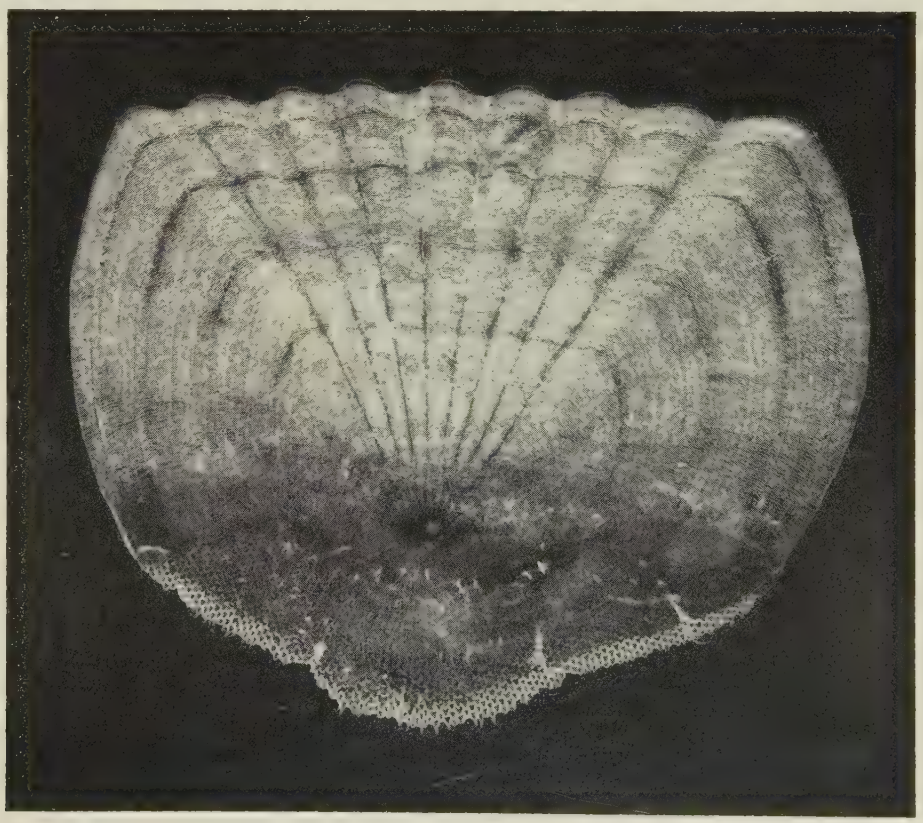

Fig. 4: Snapper scale showing four annuli. Fish length 25 cm, female, taken at Kawau Island, 26 June 1968. Direct print from scale.

Fig. 5: Snapper otolith showing four hyaline rings; from the same fish as was the scale in Fig. 4. Viewed in cross section, polished and heated as explained in the text.

size groups which could well be natural age groups. This locality was sampled irregularly from 1964 to 1970, with monthly or 2-monthly intervals (with one exception) in 1965 and 1966. Other Gulf localities were sampled less regularly to detect possible regional variations in growth rate.

Both scales and otoliths (Figs. 4 to 7) proved useful in age and growth studies.

JUVENILE AGE AND GROWTH

Scale Reading and Length-frequency Analysis

Few fish less than 10 cm in length had a distinct annulus on their scales, and most fish between 10 and 20 cm in length had 1, 2, or 3 annuli. A preliminary subjective examination of samples from the western Gulf (Kawau Island and adjacent localities) in winter 1965 showed good agreement between the age inferred from length-frequency modes and the number of annuli on the scales. This was confirmed by using scale reading to separate a length-frequency distribution into its "age group" components via an age-length key (Fig. 8).

The probability that the modal peaks did represent natural age groups was tested by following the movement of modal peaks in successive samples from the same (Kawau Island) locality (Fig. 9).

In November 1964 two size groups occurred, at 10 and 15–16 cm. They occurred again in March 1965 at 13 and 18 cm. The first (smaller) of these could be followed through to April 1966. In November 1965 it reached 15–16 cm, the size the second size group had been in November 1964. Another, smaller size group which first appeared in May 1965 could also be followed through the samples, reaching 11 cm in November 1965 and 15 cm in December 1966. These and similar trends confirmed that the size groups were in fact age groups. The second (larger) of the two original groups reached about 20 cm at the end of 1965. The good agreement of size groups in corresponding months of subsequent years suggests that the years most extensively sampled (1965–66) produced year classes with fairly typical growth trends.

There are some anomalies in Fig. 9, not of modal length values, but of poor representation or absence of certain age groups expected to be present. These are assumed to result from some behavioural separation of age groups, which caused one or more age groups to be occasionally missed from an otherwise adequate trawl sample.

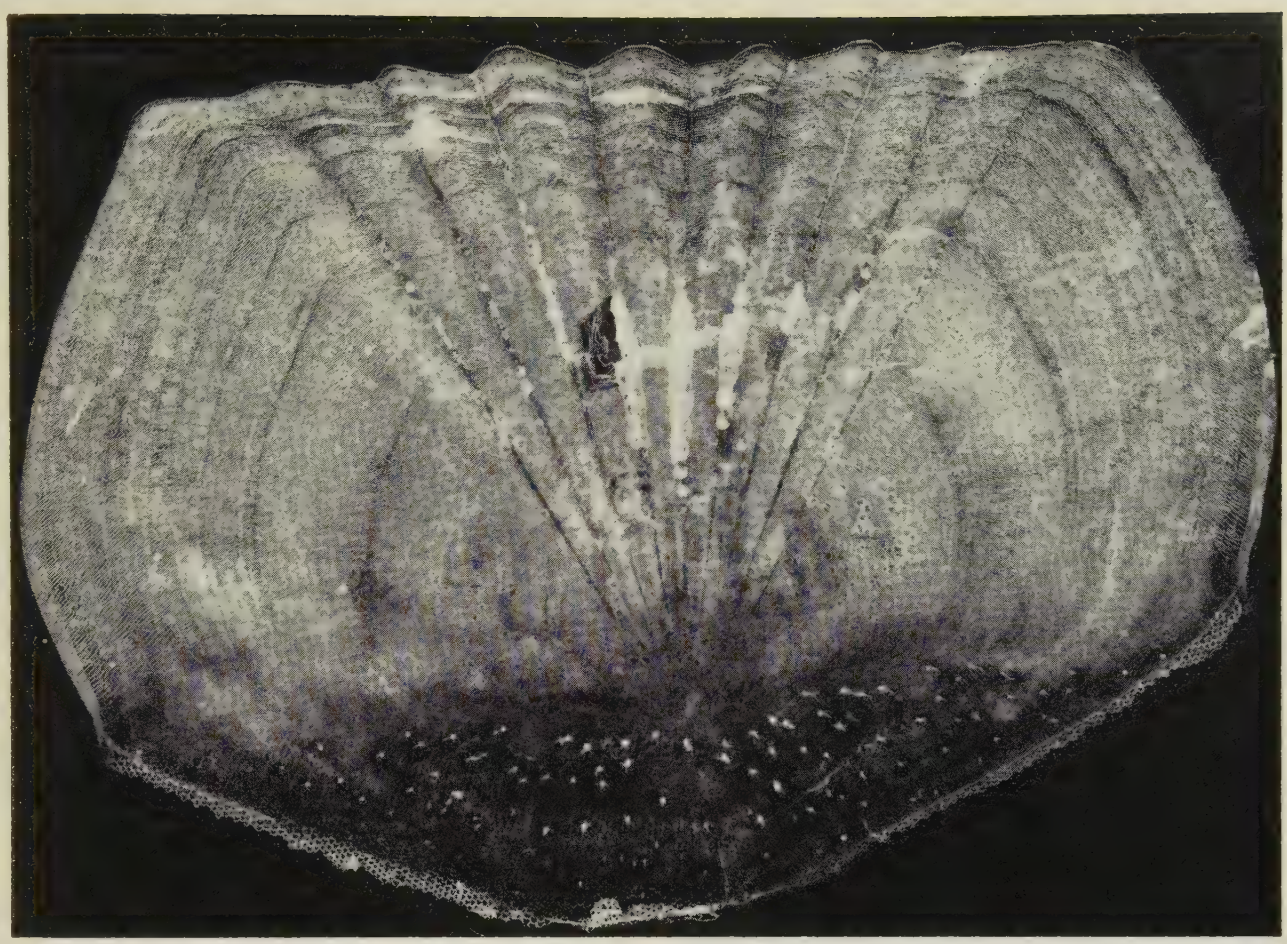

Fig. 6: Snapper scale showing 10–15 annuli. Fish length 37 cm, female, taken at Kawau Island, 26 June 1968. Direct print from scale.

Length-frequency and scale reading data considered together show that juvenile snapper at Kawau Island reach about 11, 16, and 20 cm respectively at the end of each of their first 3 calendar years of growth. At the end of their fourth year, when they begin to mature, they are 24–25 cm in length.

The size range within each age group is considerable. Fast-growing fish in their first year (0+) may equal slow-growing 1-year-old (1+) fish in size, about 13 cm, by the end of their first autumn (May–June). The older age groups have a progressively greater overlap in size.

Seasonal Growth. The data in Fig. 9 are replotted in Fig. 10 to show seasonal differences in growth more clearly, the curves being fitted by eye through estimated modal values. Modal values obtained from Cassie's (1950, 1954) method of length-frequency analysis are also shown; they are essentially similar.

The main growing season extends from November or December to about May, growth being most rapid between February and April (midsummer to early autumn), when bottom water temperatures were warmest (Paul 1968b).

Scale reading provided a quick method of ageing juvenile snapper taken in autumn and winter, the number of annuli equalling the number of completed years of life. Fish taken in spring and summer, however, had a more complex relationship between number of scale annuli and age because of seasonal growth and a variable period of annulus "formation".

Time of Annulus Formation. An annulus was observed close to the edge of the scale in juvenile snapper in November 1964 and November 1965. From May to October 1965 there was a large growth zone between the outermost annulus and the scale edge. This is shown quantitatively for scales with 1 and 2 annuli in Fig. 11, where the size of the outermost growth zone, expressed as a percentage of the preceding zone, is plotted at 2-monthly intervals from September 1964 to April 1966. Fish with small outermost zones were first taken in November 1964 as well as fish with large zones; that is, the annulus was

Fig. 7: Snapper otolith showing about 20 hyaline rings; from the same fish as was the scale in Fig. 6. Viewed in cross section, polished and heated as explained in the text.

becoming visible during that month. The width of the outermost zone increased rapidly until June and then remained fairly constant at a large size until October. In November 1965 small zones appeared again and then similarly increased in size during summer. Little or no scale growth occurred during winter, which paralleled the cessation of body growth during the same months (Fig. 10). Thus the annulus is "formed" during winter, but becomes visible only after spring growth resumes. This agrees with the general conclusions of Berg and Grimaldi (1967) on annulus formation in fishes.

It follows, also, that the annulus should be visible earlier after a mild winter and early spring than after a cold winter and late spring. Air temperatures in the Hauraki Gulf area were average to cool in 1964 and 1965 (see Fig. 36). In 1967 they were well above average from August through into spring, and in this year annuli were visible on the edges of the scales of most juvenile fish in September, 2 months earlier than in 1964 and 1965.

Thus the annulus of juvenile snapper forms about half way through each calendar year of life and becomes visible about 3 months later, the first annulus representing 6 months' growth, the second 18 months' growth, and so on. The growth zones between them represent actual growing seasons of only a few months and not whole calendar years.

Position of First Annulus. The variable position of the first annulus is a source of confusion in scale reading. Longhurst (1958) recognised two scale types, characterised by small and large first growth zones, and stated that agreement between the growth rates of the two types could be achieved only " . . . if the small inner and the large inner respectively are assumed to be the annulus formed at the end of the first year's growth". He implied that the variations in first growth zone size were due to variations in the time of spawning: a fish spawned early in the season would have a larger growth zone and vice versa. I examined more samples of scales than were available to Longhurst and in most found a wide range of first zone sizes rather than two types. One series of samples, however, did show two sizes of first growth zones, which could be related to two sizes of fish comprising one year class. Figure 12 shows that the 1966 year class at The Noises islands locality in the south-west corner of the Gulf had a bimodal length-frequency distribution when sampled as approximately 1-, 2-, and 3-year-old fish. (Apart from the bimodality, the size groups agreed well with the age groups already identified at the Kawau Island station.) Two distinct sizes of first growth zone occurred in the 1966 year class, a small zone (less

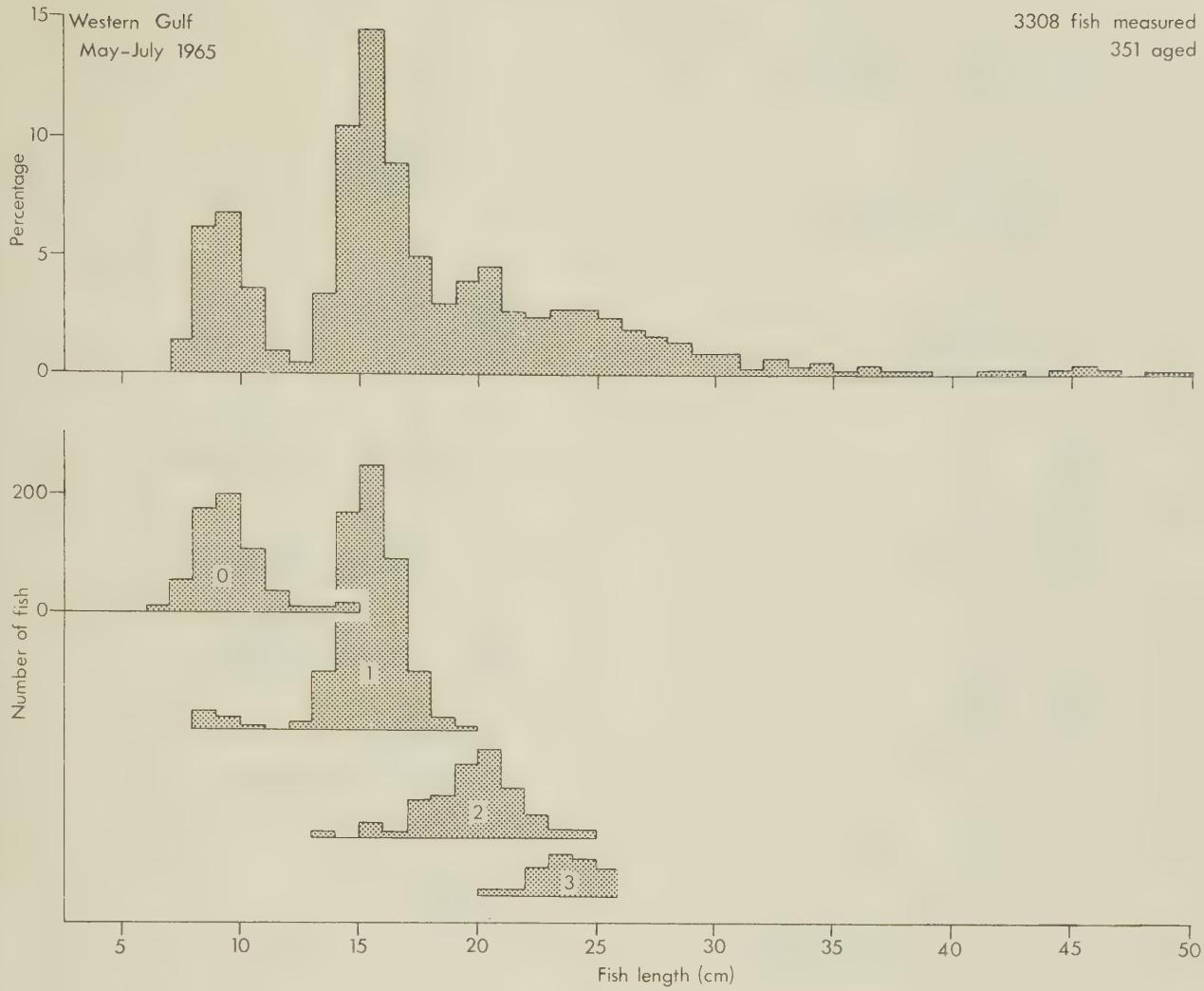

Fig. 8: Agreement of first four modes in length-frequency distribution with modal lengths of fish less than 25 cm having 0, 1, 2, and 3 scale annuli. The lower histograms were derived from the main length-frequency distribution via a stratified subsample and an age-length key. Numbers of scale annuli are shown.

than 2 mm) in fish comprising the smaller mode and a larger zone in the larger fish. This agrees with Longhurst's assumption that small zones are associated with late-spawned fish and large zones with fish spawned early. In this bulletin I accept a wide range of first growth zone sizes as valid measures of the first summer's growth.

Otolith Reading

Otoliths from small numbers of juvenile snapper were initially examined in an attempt to check on the interpretation of scales from the same fish. Subjectively, the number, spacing, and also clarity of otolith rings usually equalled those of scale annuli. This unfortunately meant that otolith reading did little to clarify scale reading and vice versa, but did suggest that both were valid for age determination of juveniles. This was confirmed by reading the scales and otoliths from the same sample of fish and separating a length-frequency distribution into its age group components via an age-length key (Fig. 13). Scales and otoliths gave virtually identical results.

ADULT AGE AND GROWTH

Description of Scale and Otolith

Scales and otoliths from large fish contain many growth rings or annuli (Figs. 6 and 7).

The scale illustrated has large growth zones between the first 3 annuli, followed by zones which decrease rapidly in size towards the scale edge. The annuli near the edge are closely crowded and some are incomplete. This is typical of most Hauraki Gulf snapper with more than 10 scale annuli. The scales

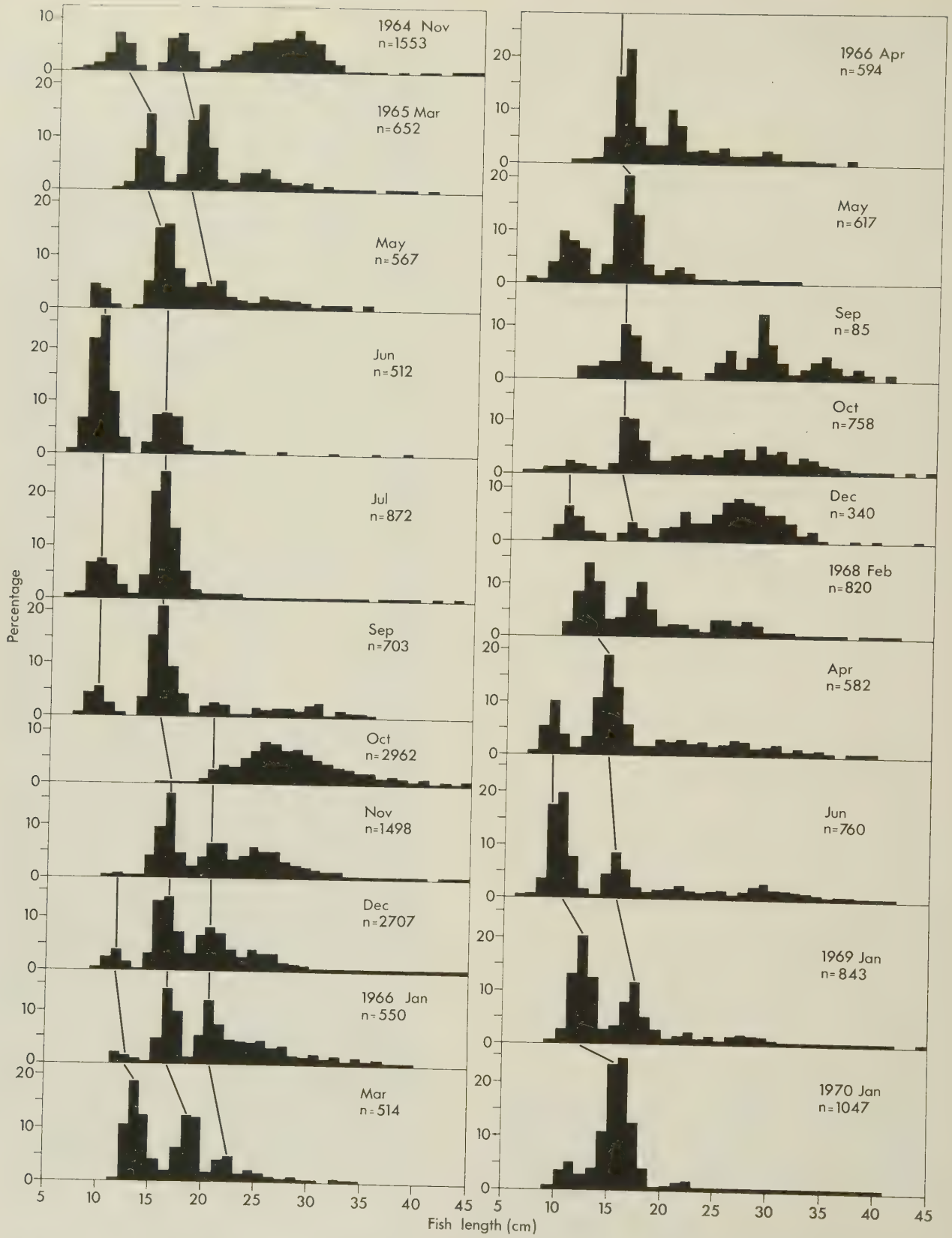

Fig. 9: Length-frequency distributions of snapper at the Kawau Island locality, 1964–70, showing movement of modes through successive samples.

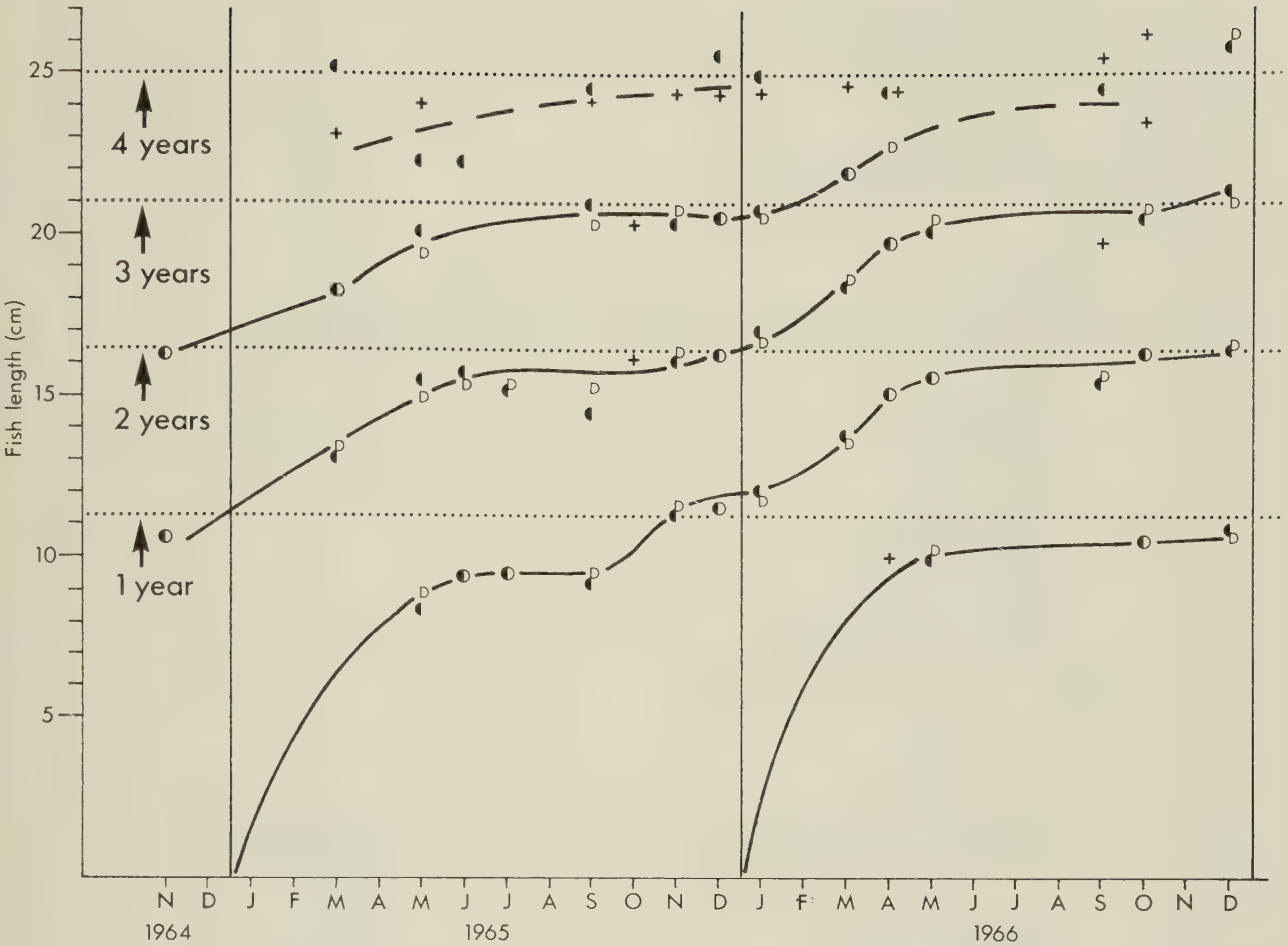

Fig. 10: Seasonal growth of snapper at the Kawau Island locality. Closed semicircles: Fish lengths from polymodal length-frequency analysis (Cassie 1950, 1954). Open semicircles: Fish modal lengths estimated by eye, distinct modes. Crosses: Fish modal lengths estimated by eye, indistinct modes. The growth curves have been fitted by eye. Based on length-frequency distributions in Fig. 9.

of a few fish examined during this study had a distinctly different appearance; their annuli were more widely spaced, and the growth zones decreased regularly in size from the innermost zone out to the scale edge. Too few of these scales were collected for a proper assessment of the phenomenon.

The sectioned otolith (Fig. 7) also has three relatively large inner growth zones, with a marked decrease in ring spacing beyond these. The outermost rings are uniform in both spacing and visibility, features that are typical of most Hauraki Gulf snapper otoliths examined.

Time of Scale Annulus Formation

Fish in their fourth and fifth years of life, about 20–25 cm in length, have mature but relatively small gonads and show growth changes consistent with the attainment of sexual maturity (see page 29 and Fig. 15). The pattern of marginal scale growth for these fish is shown separately from that of adults in Fig. 14.

The scales of 3+ and 4+ fish (Fig. 14) showed a similar trend to those of juveniles (page 21 and Fig. 11). The bimodal distribution of outermost growth zone sizes in November–December 1964 demonstrated annulus "appearance" at that time. Mean size of the outermost zone then increased until the following November–December. However, small zones were still present in March, which suggests that though annulus formation is annual and presumably represents a winter growth check, renewal of growth occurs later than in juveniles.

The scales of recognisably mature (5+ and older) fish (Fig. 14) are more difficult to interpret, mainly because the very small size and uniformity of the growth zones (Fig. 15) preclude accurate measurement and produce an artificially high number of 100% marginal increment values during most of the year. This problem aside, the greatest proportion of low values occurred in March and April 1965. The general trend of values suggests that the annulus becomes

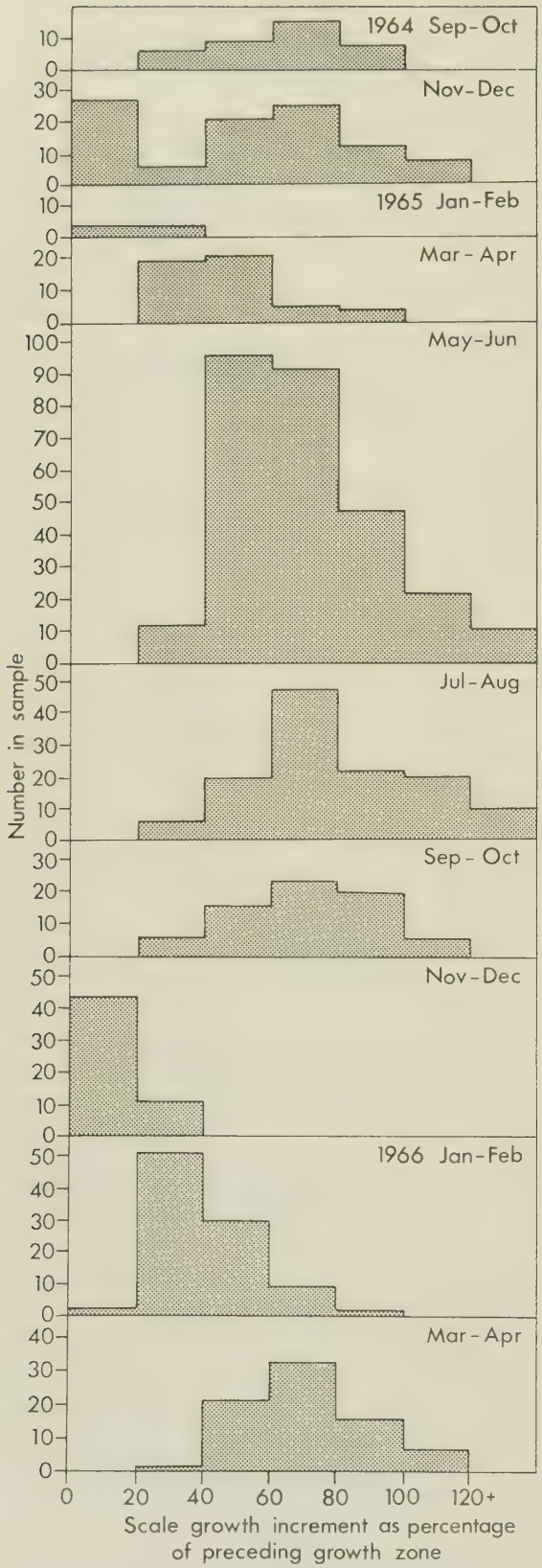

Fig. 11: Seasonal growth of outermost scale growth zone for 1+ and 2+ fish, showing time of annulus appearance.

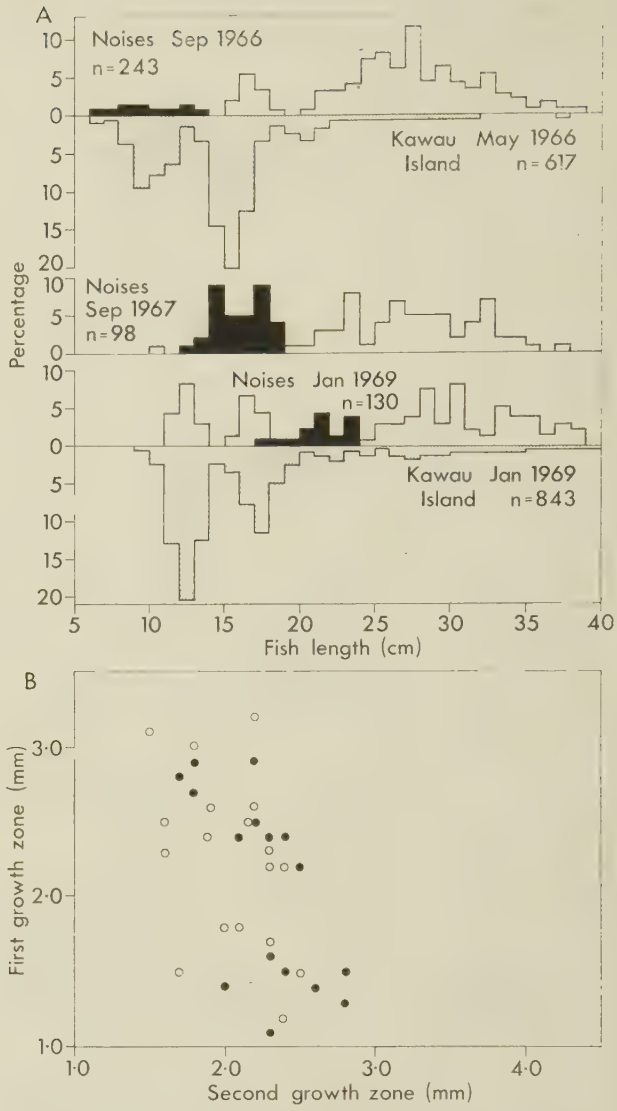

Fig. 12: Effect of bimodal length-frequency distribution of one year class on the size of the first scale growth zone. A: Bimodal length-frequency distributions of the 1966 year class (black) at The Noises islands station at three sampling periods, compared with those of Kawau Island samples. B: Size of first scale growth zone from fish in large and small modes of the 1966 year class. The upper group, above 2 mm, is from a large mode (16–18 cm in September 1967, 22–23 cm in January 1969). The lower group, below 2 mm, is from a small mode (13–15 cm in September 1967, 17–21 cm in January 1969). The solid circles represent the September 1967 sample and the open circles the January 1969 sample.

apparent in late summer or autumn, that is, later even than in the adolescent fish.

The size of successive growth zones (Fig. 15) decreased in an apparently regular manner, from 2.6 mm for the first zone to 0.2 mm for the eighth and successive zones. However, when these mean values were plotted as percentages of preceding zones it became clear that there was not a simple linear trend

Fig. 13: Agreement of first two modes in length-frequency distribution with modal lengths of fish having 0 and 1 scale annulus and otolith ring. Agreement between modal lengths of fish having 0–6 scale annuli (drawn in white) and otolith rings (in black) is also shown.

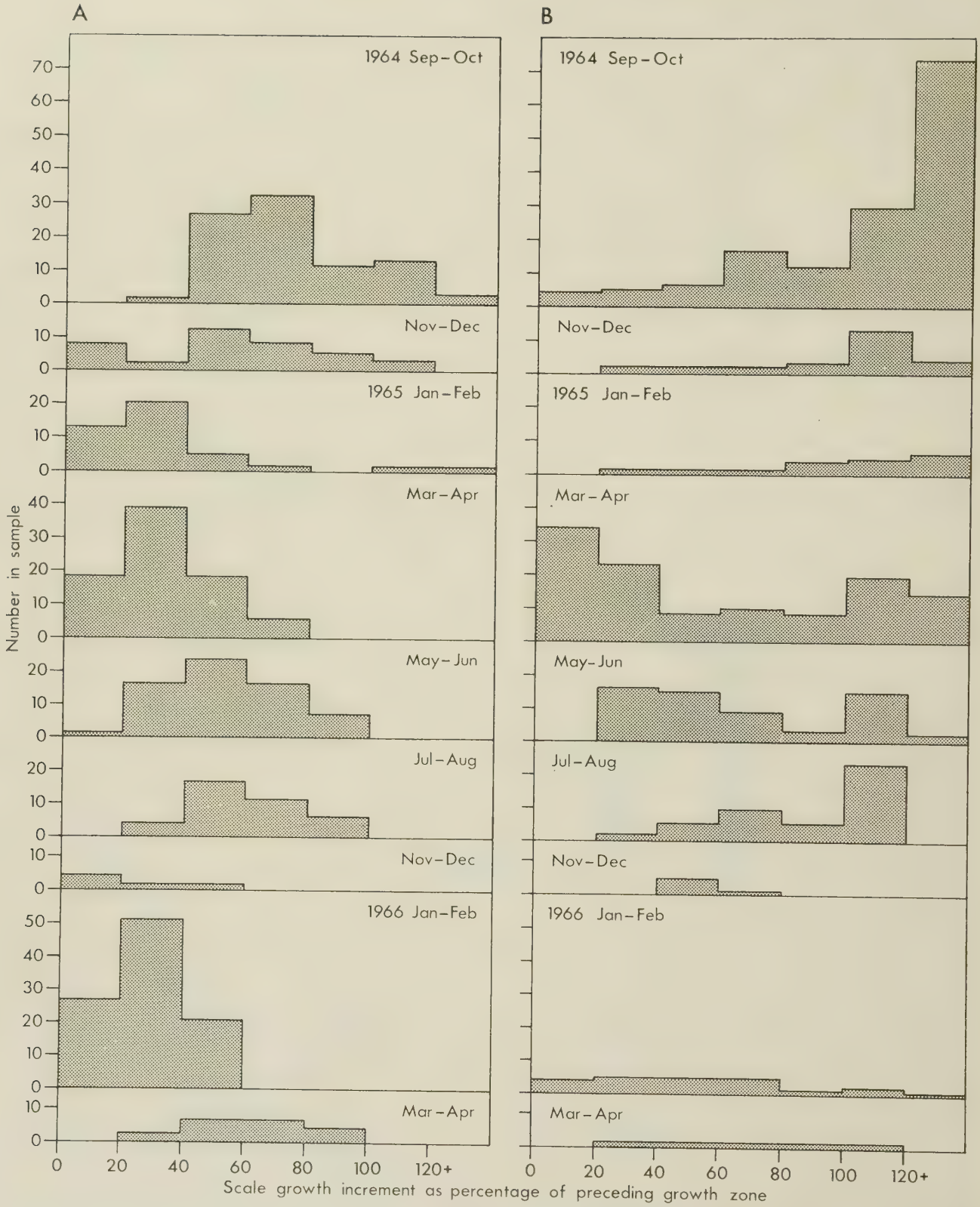

Fig. 14: Seasonal growth of outermost scale growth zone for adult snapper, showing time of annulus appearance. A: 3+ and 4+ fish. B: 5+ and older fish. No data were available for September–October 1965.

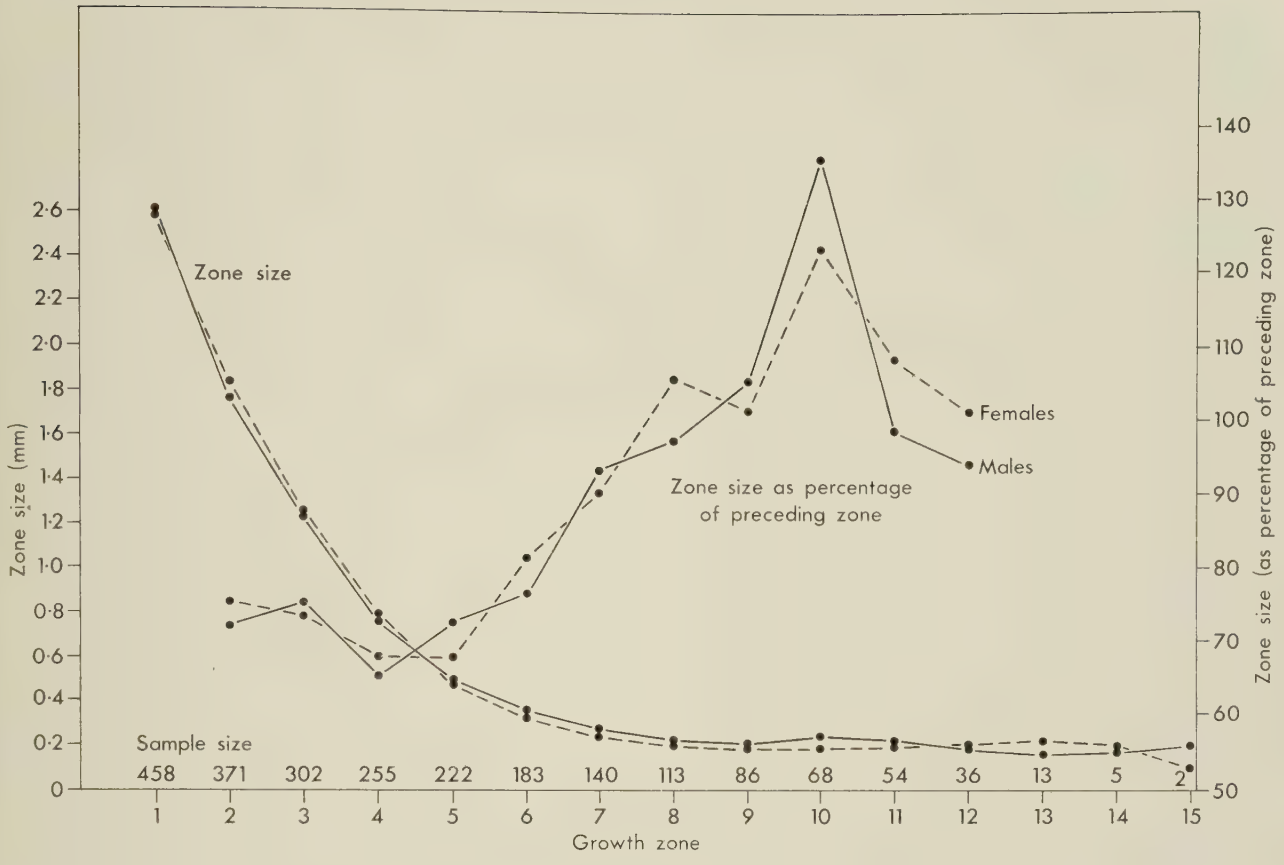
Zone size
Females
Males
Zone size as percentage
of preceding zone
Sample size
458 371 302 255 222 183 140 113 86 68 54 36 13 5 2
Zone size (mm)
Zone size (as percentage of preceding zone)
Growth zone
0 0·2 0·4 0·6 0·8 1·0 1·2 1·4 1·6 1·8 2·0 2·2 2·4 2·6
50 60 70 80 90 100 110 120 130 140
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

Fig. 15: Changes in size of scale growth zones with increasing age, both in absolute size and as a percentage of the preceding growth zone size.

towards smaller zone size. When sexes (which showed no real difference) were combined there was a decline from 74% for zones 2/1 to 67% for zones 4/3, and then a gradual increase to about 100% for zones 8/7. Beyond this point there was some variation, probably owing to a combination of small zone sizes and small samples, but general observations and measurements of older scales suggested a continuation of the 100% value. The somewhat greater decrease in mean size of zone 4 coincides with the attainment of sexual maturity. The decrease is insufficient to suggest a doubling of ring formation after maturity, but probably represents a diversion of energy from somatic growth (represented by scale growth) to reproductive development at this age. A similar temporary reduction in growth rate was shown for lake trout by Miller and Kennedy (1948), and the probability of some growth change occurring at maturity is accepted by Beverton and Holt (1957, page 100).

Although the evidence presented here is not conclusive, I interpret it as showing that the scale annulus forms only once a year in adult snapper, that it forms in winter (June–September), and that it does not show on the edge of the scale until late spring (November–December) in small adolescent fish or late summer (March–April) in mature adults.

There are two possible explanations for this delay in annulus appearance. It may be due either to the somatic growth period of adult snapper being restricted to the warm summer and autumn months after spawning or to the slower growth rate of adults, with the result that more time must elapse before the new growth zone is visible beyond the annulus.

Comparison of Scale and Otolith Readings

A sample of 195 snapper caught off Kawau Island in June 1968 was aged by scale reading and also (independently) by otolith reading. Up to age 12 (otolith ring count) there was close agreement between scale and otolith readings ($r=0.99$), with the disagreements resulting from an ambiguous ring pattern on the scale and/or otolith. Above 12 there was virtually no agreement ($r=0.05$) because of definite disagreement in ring count. Most of the fish with more than 12 otolith rings had more rings on the otolith than on the scale, as did most other large

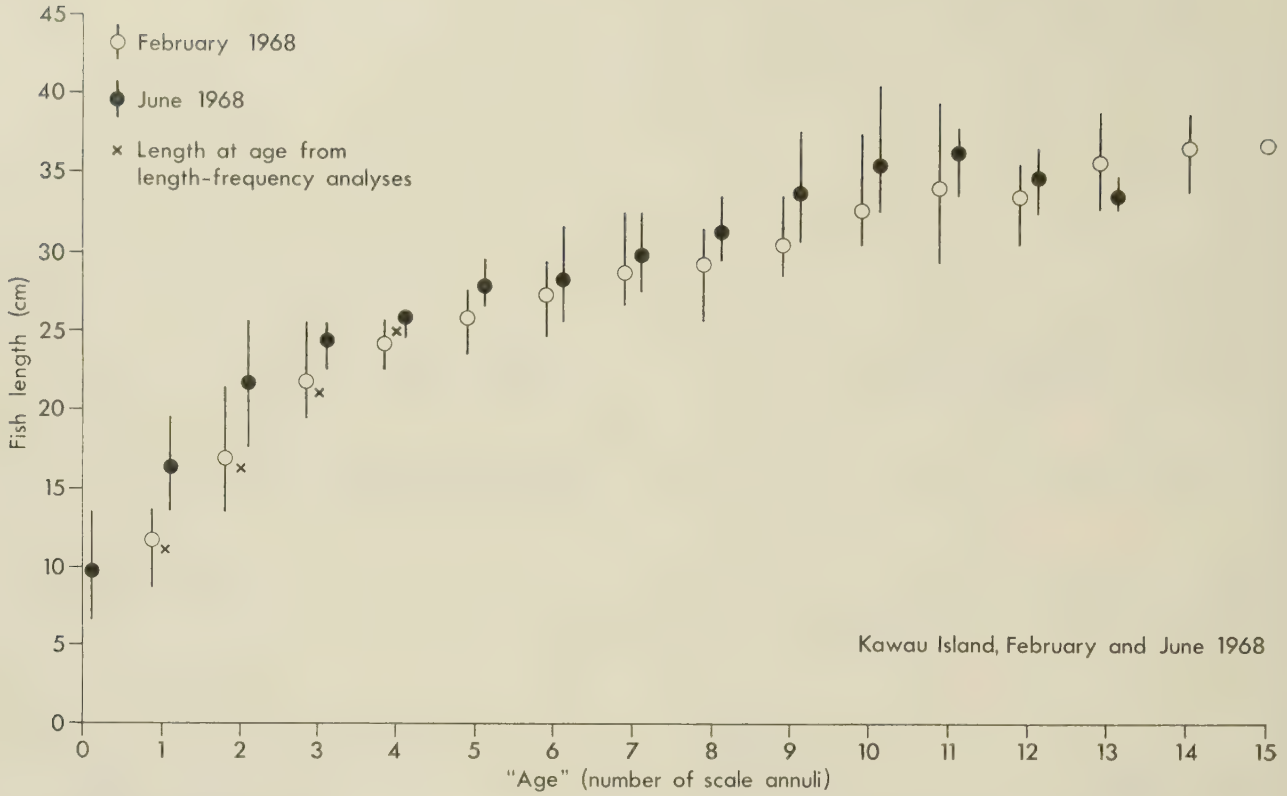
February 1968
June 1968
× Length at age from length-frequency analyses
Fish length (cm)
"Age" (number of scale annuli)
Kawau Island, February and June 1968

Fig. 16: Growth curve from age at capture, by season. Mean and range are shown. The data from length-frequency analyses are derived from Fig. 9.

snapper examined for further information on this characteristic.

The closely crowded annuli near the edge of scales from moderate to large snapper suggest that a reason for the discrepancy could be a slowing down or cessation of growth. Scale annuli are the result of interruptions in growth, and they need resumption of growth for their formation. If no growth occurs for several years, the regular annual cycle of annulus formation will be broken. Buchholz and Carlander (1963) reported that most fish in a slow-growing population of yellow bass, *Roccus mississippiensis*, failed to form annuli over 4 successive years and commented: "Failure of annulus formation in slow-growing fish of several species is believed to be more common than reported, but difficult to detect."

There is even less information on otolith ring formation in slow-growing species of fish which reach a great age. Most studies imply that the formation of rings—apart from distinctive spawning rings—is annual and state that this is difficult to prove conclusively. This assumption must also be made in this study on snapper. Thus the otolith ring count gives the true age; the difference between this and the scale annulus count indicates the number of years when little or no growth occurred and/or when no spawning (a major growth interruption) took place.

I conclude that both scale reading and otolith reading are valid for age determination up to age 12 or, to be safe, 10. Beyond this, scale reading is unreliable unless "incomplete" scales are recognised and discarded (see page 37 and Fig. 21).

Growth Curve from Age at Capture

Two samples of snapper from the Kawau Island locality were used to obtain mean length at age from scale readings (Fig. 16). The data were plotted as the range and mean of lengths for fish with the same number of scale annuli. Modal lengths for the end of the first 4 calendar growth years were derived from the length-frequency analyses in Fig. 9.

The February sample represented slightly more than a calendar year's growth and gave mean lengths that were reached part way through the spring–autumn growing season. The June sample gave mean lengths from the end of the same growing season. This difference in sampling time accounted for the difference between the two sets of data, which was most apparent for ages 1–3. The mean lengths from the June sample were higher, being taken from fish which

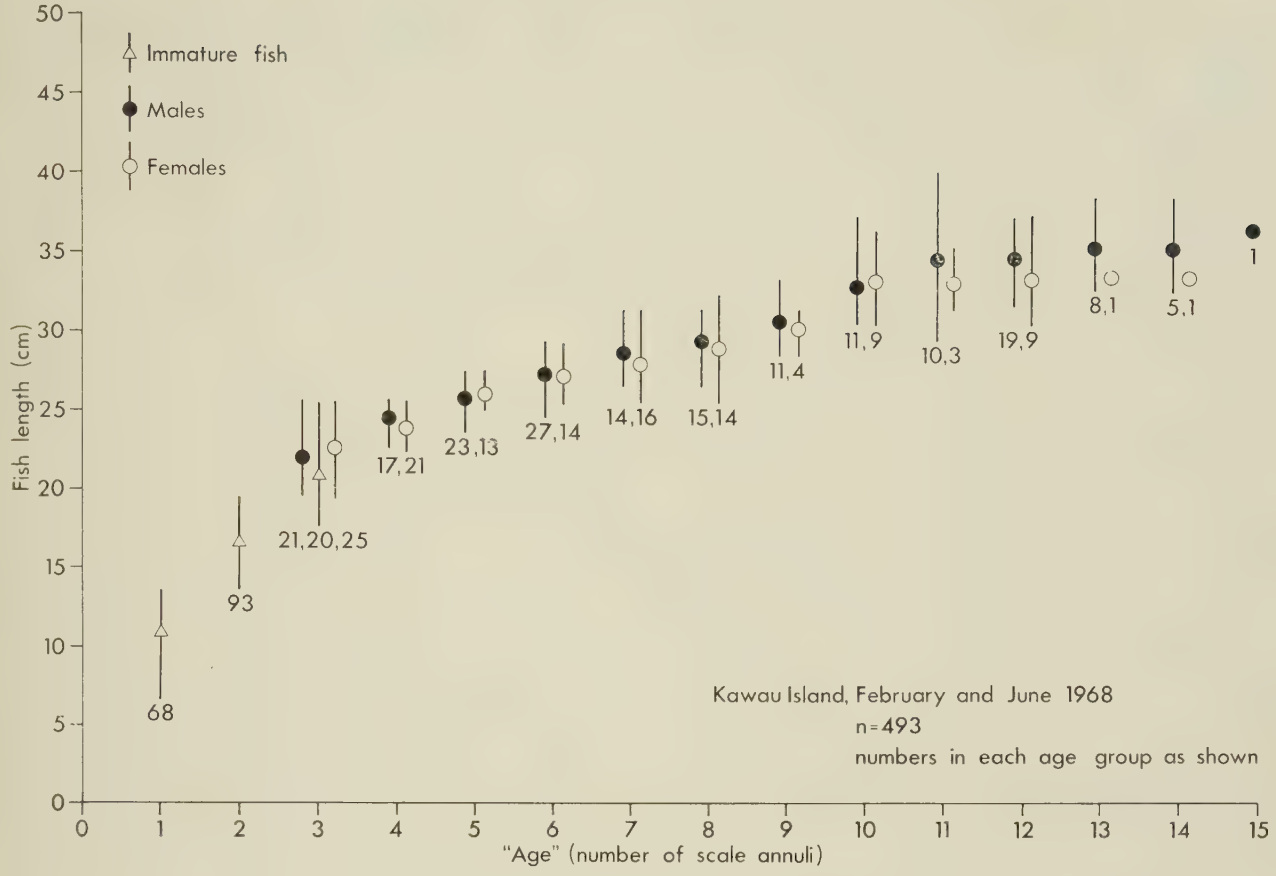

Fig. 17: Growth curve from age at capture, by sex. Mean and range are shown.

would shortly form their next scale annulus. In fact, though only 4 months separated the samples, the June fish were almost one growth season older and larger than the February fish with the same annulus count. This can be demonstrated in Fig. 16, where, if the June values are moved 1 unit to the right, the mean lengths of June fish with n annuli agree mostly with those of February fish with $n+1$ annuli. For the first two age groups (1 and 2 annuli in February) the February lengths were slightly larger than the "preceding" June lengths, perhaps an indication that the younger juveniles begin spring growth earlier than the older juveniles.

The modal lengths of juveniles from length-frequency analyses (11, 16, and 20 cm; see page 21 and Fig. 9) agree well with the February mean lengths at age from scale reading. Both represent approximately calendar year growth values. The distinction between these and natural growth season values (such as the June values above or lengths back calculated from scale annulus positions) should be considered when growth data are compared.

The February and June samples were combined to show mean lengths at the end of each growth season, with immature fish, mature males, and mature females shown separately (Fig. 17). As has already been shown (Fig. 15), the male and female values correspond closely, though there were insufficient fish in the older groups for a good comparison.

Back Calculation of Growth from Scales

One of the most convenient methods of determining the growth rate of an individual fish is to back calculate its lengths at previous ages from the relative position of annuli on the scales. This method is based on the assumption that the scale grows at a rate related to growth in length of the fish. In this way much information on growth trends in a particular stock can be obtained from a fairly small sample of fish. The method has been widely used on a large number of species (Chugunova 1959, Hile 1970) with varying success. Previous attempts to back calculate the growth rate of New Zealand snapper (Cassie 1956c, Longhurst 1958) were unsuccessful, but with more extensive data and a slightly different technique I have obtained useful results.

Fish Length-Scale Size Relationship. The fish length-scale size relationship is curvilinear (Fig. 18). The scales become relatively larger, compared with

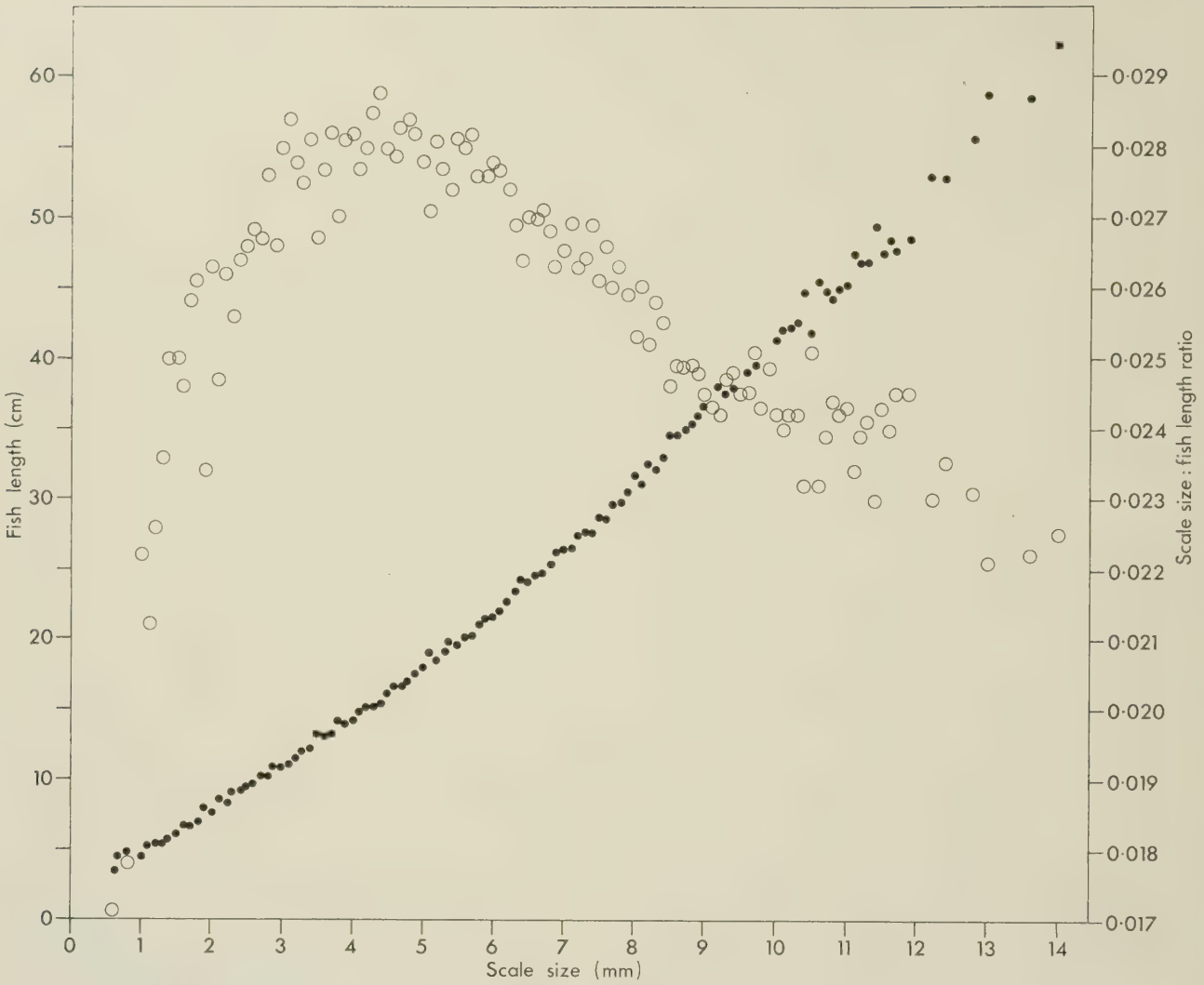

Fig. 18: Fish length-scale size relationship. Solid circles: Fish lengths at each 0.1-mm increment in scale size. Open circles: Scale size : fish length ratio at each 0.1-mm increment in scale size.

fish length, until they reach 4 mm (corresponding to a fish length of 15 cm); thereafter they decrease in relative size. The early relative increase in scale size may be due to the scales being formed after the fish started growing and then growing faster for a short time to "catch up". The curvilinear regression of scale size on the scale size:fish length ratio can be extrapolated to intercept the fish length axis at a positive value (about 15 mm), which suggests that the scales formed when the fish was at about this length. The reason for the subsequent decrease in relative scale size is uncertain, but it could well represent changing body proportions (see Fig. 1).

The curvilinear relationship and positive intercept must both be taken into account when back calculating fish lengths. Techniques of back calculation in which this is not done were investigated, but they gave erroneous results similar to those obtained by Cassie and Longhurst.

Back Calculation with Empirical Data and a Nomograph. The simplest method of obtaining a fish length-scale size regression is to draw a free-hand curve through the actual data. This method requires numerous accurate measurements over a wide size range of fish, but avoids the systematic errors caused by failure of the fish length-scale size data to conform to a particular equation (Hile 1970). It is appropriate for the present account of back-calculated snapper growth, because 1500 scale measurements over a wide size range of fish are available and because the regression curve (Fig. 18) is complex.

A free-hand curve drawn through the mean fish length-scale size measurements in Fig. 18 can be used to construct a nomograph as described by Hile (1950,

1970). The nomograph simplifies back calculation by taking into account both the curvilinear fish length-scale size relationship and the positive intercept on the fish length axis and allows the lengths of a fish at successive annuli to be determined from a single setting of a movable arm.

It was assumed that the samples of Hauraki Gulf snapper on which the nomograph was based were taken from sufficient localities to represent a "generalised" Hauraki Gulf snapper stock at the time of sampling.

Scale readings (focus to successive annulus measurements) from the February and June 1968 samples were converted to back-calculated lengths by this method, and the results were plotted in a similar way to those in Fig. 4 in Cassie (1956c) except that they were grouped by "age" rather than by fish length (Fig. 19).

Most of the lower values show good agreement with observed winter modal lengths (see Table 2).

The slope and irregularities of the higher lines clearly reflect the mean length at capture of fish in each "age" group. The fish with 11 annuli, for example, were on average larger than those with 12 annuli, and their L_n values from L_3 (=maturity) onwards were correspondingly larger. That is, fish that are large for their age back calculate larger than average L values and vice versa.

A comparison can be made between mean back-calculated lengths (mean L_1, L_2, L_3, etc.) and mean

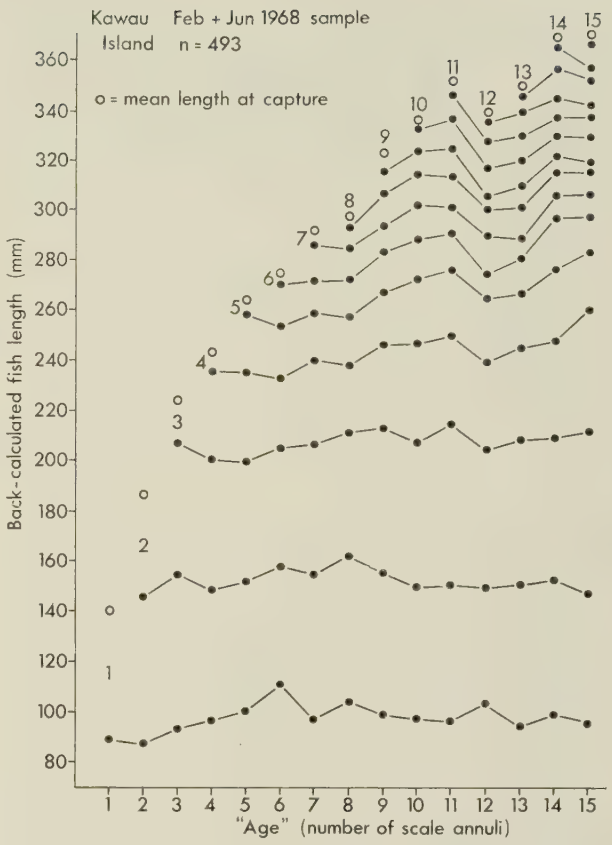

Fig. 19: Variation in back-calculated L_n values with increasing number of scale annuli (based on nomograph). Numbers of fish in each "age group" are listed in Table 2. Mean length at capture is by year class, from Table 2.

TABLE 2: Comparison of mean back-calculated lengths with measured lengths at capture, based on February and June 1968 Kawau Island samples.

Mean back-calculated length by No. of annuli*			Measured lengths at capture: Mean length by year class (=No. of annuli)†				Mean length by growth season‡			Observed modal length in winter of first three ages (from Fig. 10)	
No. of annuli	Mean length (mm)	No.	Year class	No. of annuli	Mean length (mm)	No.	Growth season	Mean length (mm)	No.	Growth season	Modal length (mm)
			1968§	0	98	37					
1	96	457	1967	1	140	65	1	106	68	1	95
2	152	392	1966	2	186	91	2	166	93	2	155
3	207	301	1965	3	225	47	3	218	66	3	205
4	240	254	1964	4	244	33	4	242	39	–‖	–
5	262	221	1963	5	264	39	5	258	36	–	–
6	278	182	1962	6	275	43	6	274	41	–	–
7	292	139	1961	7	291	27	7	284	30	–	–
8	303	112	1960	8	297	27	8	294	29	–	–
9	315	85	1959	9	322	18	9	310	15	–	–
10	326	67	1958	10	334	14	10	332	20	–	–
11	334	53	1957	11	351	18	11	345	13	–	–
12	337	35	1956	12	338	23	12	344	28	–	–
13	348	12	1955	13	348	8	13	352	9	–	–
14	363	4	1954	14	365	3	14	350	6	–	–
15	365	1	1953	15	365	1	15	365	1	–	–

* Means of horizontal lines in Fig. 19.

† For example, February fish with 1 annulus + June fish with 1 annulus = 1967 year class, but are separated by almost one growth season. Mean lengths are shown in Fig. 19.

‡ For example, February fish with 1 annulus + June fish with no annulus = fish approximately at end of one growth season.

§ June sample only.

‖ – indicates insufficient data.

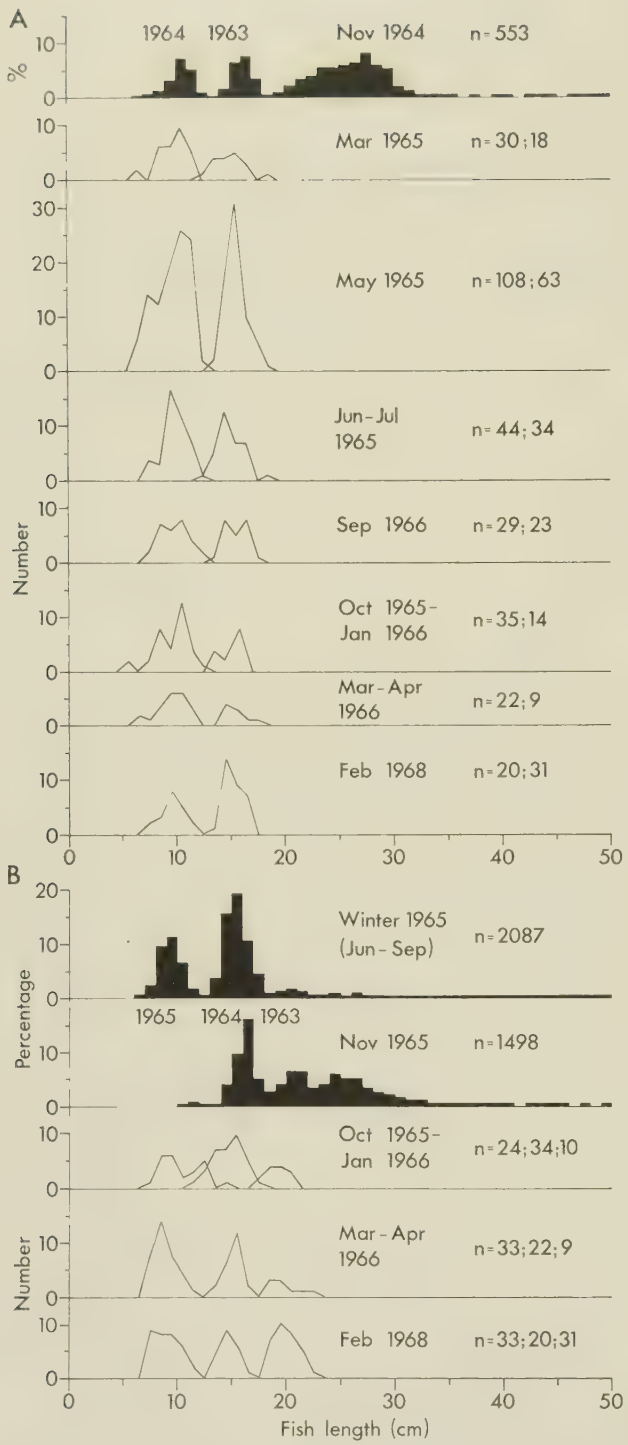

Fig. 20: Comparison of back-calculated lengths with observed lengths at (winter) annulus formation. A: Comparison of L_1 values of 1964 year class, and L_2 values of 1963 year class, with modal lengths of these year classes in spring (November) 1964 (no winter data are available; modal lengths would be slightly smaller than those in spring). B: Comparison of L_1 values of 1965 year class, L_2 values of 1964 year class, and L_3 values of 1963 year class, with modal lengths of these year classes in winter (June–September) and spring (November) 1965.

TABLE 3: Variation in growth rate of juvenile snapper at three stations in the Hauraki Gulf—Kawau Island, Mahurangi Harbour entrance, and Motuihe Channel, Motutapu Island.

	Year class			
Sampling period	1965	1964	1963	Station
1964 November	–	10.5	16.0	Kawau
	–	11.5	17.5	Motuihe
1965 May	9.0	15.0	19.5	Kawau
	9.0*	16.0	21.5	Mahurangi
	–	16.0	21.5	Motuihe
July	9.5	15.5	–	Kawau
	8.0*	16.5	–	Mahurangi
	10.5	16.0	21.5	Motuihe
September	9.5	15.5	20.5	Kawau
	10.5	17.0	22.5	Mahurangi
	9.0*	16.0	21.5	Motuihe
November	11.5	16.5	20.5	Kawau
	11.0*	17.5	22.5	Mahurangi
	12.0	17.0	22.0	Motuihe
December	–	–	20.5	Kawau
	–	–	23.0	Mahurangi
1966 January	12.5	17.0	20.5	Kawau
	–	19.0	–	Mahurangi
	14.0	–	22.5	Motuihe
March	13.5	18.5	22.0	Kawau
	14.5	20.5	24.0	Mahurangi
	15.5	21.0	24.0	Motuihe
May	15.5	–	–	Kawau
	17.0	–	–	Motuihe

Modal lengths are estimated to nearest 0.5 cm by eye from length-frequency distributions; see Fig. 10 for relationship between estimated and calculated modal lengths in the Kawau samples. In general the Mahurangi and Motuihe modal lengths are greater than those from Kawau; exceptions are marked with an asterisk.

A dash indicates insufficient fish or that the modal length of the year class is inadequately defined.

lengths at capture by (a) number of annuli and (b) number of growing seasons (Table 2). Mean back-calculated lengths are more regularly spaced than are lengths at capture, because they average out the growth history of several year classes. Lengths at capture reflect the growth rate of single year classes, which can—where sufficient data are available—be compared with the mean growth rate for the region to detect any changes in growth rate with time. Allowance must, of course, be made for the fact that lengths at capture will be greater than back-calculated lengths, because they include some fish growth after the time of annulus formation.

The back calculation technique can also be tested by back calculating L_1, L_2, etc., from single year classes at successive sampling periods and comparing the size distribution of the L_n values with the observed length-frequency distribution of the year classes at the time of annulus formation. Data from the 1963, 1964, and 1965 year classes of Hauraki Gulf snapper (Fig. 20) show good agreement between the back-calculated and observed lengths.

Back calculation of snapper growth from suitable scales can thus be regarded as reliable and can be simplified by use of a nomograph.

VARIATIONS IN GROWTH RATE

Juvenile Growth

Regional Variations in Juvenile Growth. It soon became apparent during this study that the modal size of juvenile age groups varied between localities.

At two localities in particular, Mahurangi Harbour (two stations) and Motutapu, juvenile snapper were consistently 1–2 cm larger than at Kawau Island (Table 3). The supposition that the Mahurangi and Motutapu values were greater than Kawau Island values was tested with the null hypothesis that there was no difference. Kawau Island modes equalled or were greater than Mahurangi or Motutapu modes only thrice in 35 comparisons, a probability much less than 5%; thus the observed modal growth differences were significant.

This feature was investigated further by using the nomograph to back calculate the juvenile growth rate of separate selected year classes from Kawau Island, Mahurangi Harbour entrance, and Motutapu (Table 4). (The nomograph was based on combined samples from these and other localities and would thus average out rather than create any variations in the data.) The mean values in Table 4 show that by the end of the second (growth) year the Mahurangi and Motutapu fish were 6–11 mm larger than Kawau Island fish, and by the end of the third year they were 12–18 mm larger.

Annual Variations in Juvenile Growth. During the spring, summer, and autumn of 1961–62 first-year growth of the 1962 year class and second-year growth of the 1961 year class were greater by 10–15 mm than that of adjacent year classes (Table 4). That summer in the Hauraki Gulf was one of the warmest and calmest on record (New Zealand Meteorological Service 1964) (see Fig. 36). As sea and air temperatures in the Gulf are closely related (de Lisle 1965, Paul 1968b), it is reasonable to assume that in the shallow south-west Gulf feeding and growth conditions were better than average.

Adult Growth

Regional Variations in Adult Growth. The growth rates of snapper from six localities, from Horn Rock in the outer Gulf to a shallow Firth of Thames station, were determined (Tables 5 and 6). These can be grouped into three regions: the sheltered Firth of Thames, the more open waters of the inner Gulf, and the exposed outer Gulf. Such a grouping should reveal any growth differences which were there. If the trend shown by juveniles continued, growth would be fastest in the Firth of Thames and slowest in the outer Gulf. This possibility was tested with the null hypothesis

TABLE 4: Mean juvenile growth of several year classes of snapper at three localities in the shallow south-west region of the Hauraki Gulf, based on nomograph back calculations.

Locality	Year class	Growth in 1st year (mm)	No. in sample	Growth in 2nd year (mm)	No. in sample	Growth in 3rd year (mm)	No. in sample	Growth in 4th year (mm)	No. in sample
Kawau Island and Tiritiri Matangi	1961	98	6	63	6	44	6	35	6
	1962	111	29	54	29	51	29	28	10
	1963	99	109	52	109	45	12		
	1964	98	139	50	24				
	1965	91	20						
	Mean growth*	99, 99	303	53, 55	168	49, 47	47	31, 32	16
	Mean cumulative length	99, 99		152, 154		201, 201		232, 233	
Mahurangi Harbour entrance	1961	89	15	76	15	57	15	30	15
	1962	113	19	61	19	50	19	26	1
	1963	94	11	67	11	53	5		
	1964	89	50	60	6				
	1965	86	12						
	Mean growth	93, 94	107	67, 66	51	53, 53	39	30, 28	16
	Mean cumulative length	93, 94		160, 160		213, 213		242, 241	
Motuihe Channel, Motutapu Island	1961	–†	–	–	–	–	–	–	–
	1962	116	14	49	14	54	14	–	–
	1963	103	28	58	28	54	11		
	1964	101	32	67	2				
	1965	107	3						
	Mean growth	105, 107	77	56, 58	44	54, 54	25		
	Mean cumulative length	105, 107		161, 165		215, 219			

* Weighted mean and simple mean of combined year classes are given in that order; mean cumulative lengths are similarly arranged.

† – indicates insufficient data.

TABLE 5: Variation in growth rate, from age at capture, of adult Hauraki Gulf snapper.

LOCALITIES

Age (years)	Firth Length (cm)* Mean	Range	Lake Length (cm) Mean	Range	Mahurangi Hr entrance† Length (cm) Mean	Range	Waiheke-Coromandel Length (cm) Mean	Range	Kawau Island Length (cm) Mean	Range	Horn Rock Length (cm) Mean	Range
3	24.9	20–27 (25)‡	–§	–	21.3	20–21 (5)	21.9	18–25 (48)	22.0	18–24 (44)	21.3	18–24 (41)
4	27.9	26–29 (11)	–	–	25.1	23–26 (17)	25.4	23–27 (22)	24.5	21–26 (18)	23.7	21–25 (13)
5	29.5	27–31 (8)	–	–	27.5	26–28 (7)	28.0	26–29 (16)	26.8	24–28 (15)	25.7	23–27 (6)
6	31.0	28–34 (8)	28.2	26–29 (3)	28.5	26–29 (11)	28.4	26–30 (8)	27.9	26–30 (13)	27.2	24–29 (6)
7	32.3	30–37 (23)	30.1	28–32 (20)	30.0	28–31 (6)	28.9	26–31 (13)	29.4	27–32 (17)	27.9	25–32 (18)
8	34.4	32–38 (12)	31.0	29–33 (8)	30.0	28–32 (6)	30.1	27–33 (13)	30.1	27–32 (12)	28.7	25–33 (19)
9	35.5	32–38 (13)	32.4	28–36 (16)	32.5	30–33 (5)	32.0	28–34 (10)	30.6	28–32 (6)	31.5	29–34 (15)
10	35.5	35 (1)	32.0	31–33 (4)	35.0	33–39 (6)	31.5	28–34 (2)	34.0	33–34 (2)	32.0	29–34 (8)

REGIONS

	Firth of Thames Length (cm) Mean	Range	Inner Gulf Length (cm) Mean	Range	Outer Gulf Length (cm) Mean	Range
3	24.9	20–27 (25)	21.9	18–25 (97)	21.3	18–24 (41)
4	27.9	26–29 (11)	25.0	21–27 (57)	23.7	21–25 (13)
5	29.5	27–31 (8)	27.2	24–29 (28)	25.7	23–27 (6)
6	30.2	28–34 (11)	28.2	26–30 (32)	27.2	24–29 (6)
7	31.3	28–37 (43)	29.3	26–32 (36)	27.9	25–32 (18)
8	33.0	29–38 (20)	30.1	27–33 (31)	28.7	25–33 (19)
9	33.9	28–38 (29)	31.7	28–33 (21)	31.5	29–34 (15)
10	32.7	31–35 (5)	34.1	28–39 (10)	32.0	29–34 (8)

* Range given as original measurements; 0.5 cm added in calculation of mean.

† Mahurangi sample taken in June 1965; all other samples collected in January 1969.

‡ Numbers at each age in parentheses.

§ – indicates no data.

TABLE 6: Variation in growth rate of adult snapper collected in the Hauraki Gulf in January 1969, shown by mean and range of lengths of the 1962 year class, which have been calculated from scale reading and nomograph.

LOCALITIES

L_n*	Firth Length (cm)† Mean	Range	Lake Length (cm) Mean	Range	Waiheke-Coromandel Length (cm) Mean	Range	Kawau Island Length (cm) Mean	Range	Horn Rock Length (cm) Mean	Range
L_3	21.9	18–26	21.6	17–25	21.7	20–23	21.5	18–25	20.7	18–24
L_4	27.1	22–29	24.9	21–29	24.5	21–26	24.6	22–27	23.1	20–26
L_5	29.8	25–33	27.6	25–30	26.6	24–28	26.5	24–29	25.1	22–29
L_6	31.3	27–35	29.0	27–31	27.8	25–29	27.9	25–31	26.6	24–30
L	32.7	30–37	30.1	28–32	28.8	26–31	29.4	27–32	27.9	25–32
	No.=19		No.=20		No.=12		No.=17		No.=18	

REGIONS

	Firth of Thames Length (cm) Mean	Range	Inner Gulf Length (cm) Mean	Range	Outer Gulf Length (cm) Mean	Range
L_3	22.2	17–26	21.6	18–25	20.7	18–24
L_4	26.0	21–29	24.6	21–27	23.1	20–26
L_5	28.7	25–33	26.6	24–29	25.1	22–29
L_6	30.1	27–35	27.9	25–31	26.6	24–30
L	31.4	28–37	29.2	26–32	27.9	25–32
	No.=39		No.=29		No.=18	

* Back-calculated lengths at scale annuli 3–6.

† Range given as original measurements; 0.5 cm added in nomograph back calculations.

that there was no significant difference in mean growth rate between the three regions. Then the probability of observing the arrangement that Firth growth is greater than inner Gulf growth and inner Gulf growth is greater than outer Gulf growth at any age is 1/8. At the 5% significance level there must be four deviations from this pattern for eight sets of observations and two for five sets. In fact, there was one in eight sets (Table 5) and nil in five sets (Table 6); thus the hypothesis is rejected and a real difference in growth assumed.

There is not a simple relationship between adult growth rate and depth; Kawau Island and Mahurangi Harbour fish were taken from different depths, but had similar growth rates. Presumably the fish in the inner Gulf move freely between the open Gulf waters and the shallow marginal feeding grounds. However, the higher growth rate observed in Firth of Thames snapper suggests that these fish may comprise a stock which remains reasonably distinct from snapper in the inner and outer Gulf.

These differences in growth are small, apply to means rather than to individual fish (which show a considerable range of growth rates), and are most obvious in Firth of Thames fish. Most snapper available to the commercial trawl and Danish seine fishery inhabit open water and would have a mean growth rate similar to that described for inner and outer Gulf snapper in Tables 5 and 6.

Several of the scales from large fish in the samples discussed above had crowded annuli near the scale edge (Table 7), similar to those previously found (page 30) to give underestimates of age. There was a greater proportion of these from Firth of Thames stations.

Comparison of scale and otolith readings from a subsequent sample collected at the Firth of Thames entrance (Lake locality) showed that almost all fish 12 years and older had scale and otolith ring counts which differed greatly from each other (Fig. 21). This characteristic has been assumed (page 30) to represent periods of little or no growth. At first sight this appears to conflict with the finding that growth up to age 10 is more rapid in the Firth than at other localities. However, in terms of fish size, population structure, and apparent abundance Firth snapper differ from those of the rest of the Hauraki Gulf (unpublished data); further work to clarify these differences is needed before a definitive statement on the growth rate of Firth snapper can be made.

TABLE 7: Numbers of older snapper (12 or more otolith rings) at several Hauraki Gulf stations, January 1969, with discrepancies of two rings or more between scale and otolith readings.

Station	Total No. in sample	No. of older fish (12 or more otolith rings)	Fish with ring count discrepancies (% of older fish)
Horn Rock	267	62	1.6
Kawau Island	219	29	20.6
Firth	138	21	23.8
Waiheke-Coromandel	201	27	51.7
Lake	136	73	91.8
Lake (March–April 1970)	118	28	85.7

Further evidence of growth rate variation in adult Hauraki Gulf snapper is shown by the age determinations (otolith ring count) of 198 snapper caught by Danish seining in the inner Gulf during the spawning season (Fig. 22). There is a wide spread of ages at each length; a 30-cm fish could be from 5 to 15 years old and a 35-cm fish from 8 to 34. In this sample many fish older than 10 also showed differences between scale and otolith readings, the criterion used above for slow-growing ("stunted") fish. These fish, defined in this particular sample by an otolith-scale reading difference of more than 20% and identified separately in Fig. 22, do in fact have a slower growth rate than the other fish.

In the original data there was also some evidence of a bimodal length distribution at ages 9–11. The smaller modes coincided with the growth curve previously established for Kawau Island fish. The larger modes represent faster-growing fish whose origin is unknown; they may be fast-growing Firth of Thames fish which moved out into the Gulf to spawn or they may be fish from an area outside the Hauraki Gulf which moved in to spawn.

Annual Variations in Adult Growth. The differences between scale and otolith ring counts suggest that adult growth may decline or cease for some years at certain localities. Differences between back-calculated mean lengths and mean lengths at capture (Table 2) could also be used to give evidence of this.

General Features of Snapper Growth

Although geographical and temporal variations in the growth rate of snapper have been demonstrated, all the available evidence (page 35, unpublished data, Vooren and Coombs in press) suggests that the growth rate of fish taken by trawl near Kawau Island is representative of the snapper on the main Hauraki Gulf trawling and Danish seining grounds. Nevertheless, because variations do occur, the growth section in this paper does not conclude with quantitative growth equations and parameters which can be used as a basis for subsequent work on recruitment, yields,

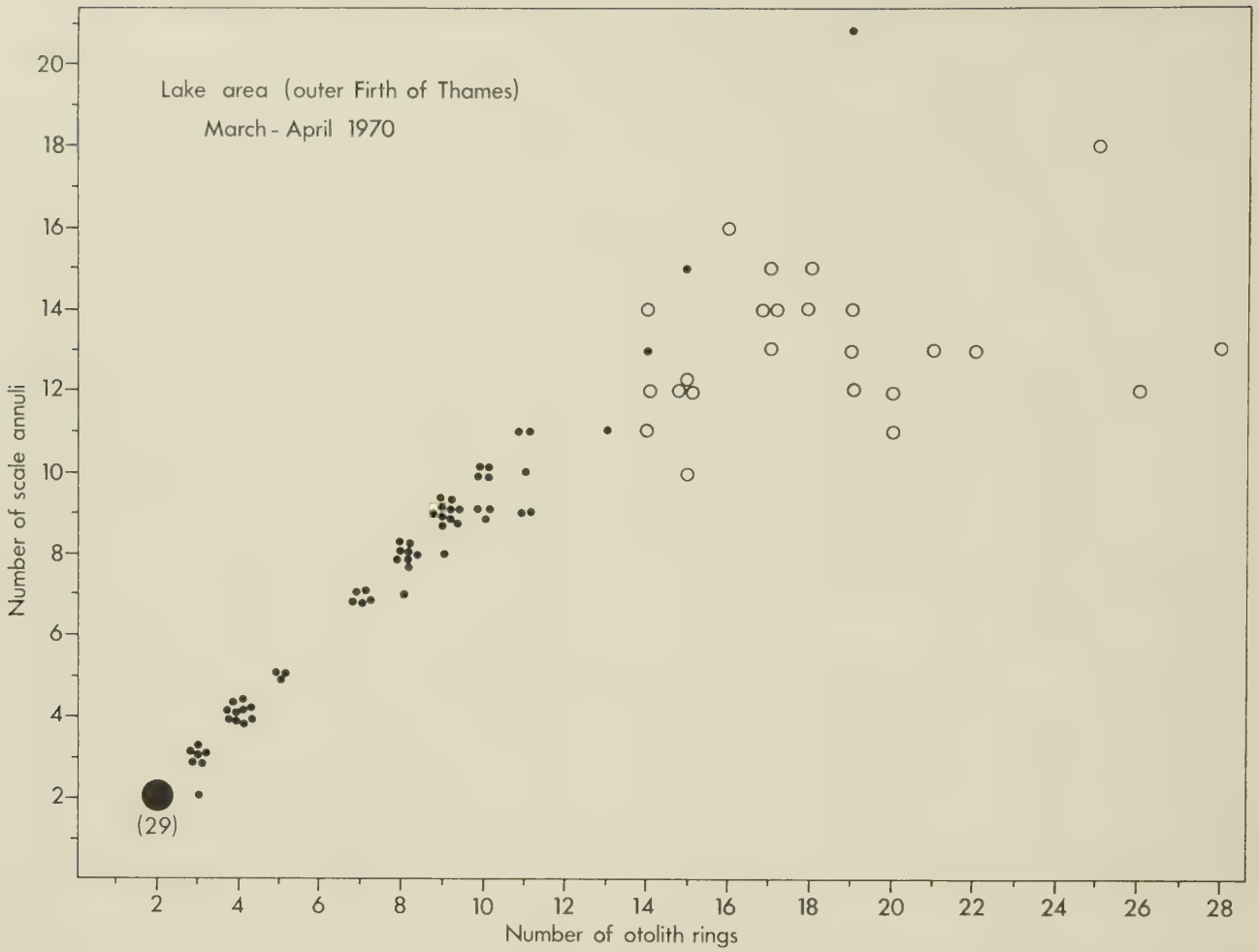

Fig. 21: Comparison of scale and otolith age readings from snapper caught at the Lake locality, March–April 1970. Solid circles: Scales subjectively judged to be "normal"; n=90. Open circles: Scales subjectively judged to have an incomplete series of annuli; n=24.

and mortalities. These must be calculated directly from appropriate samples obtained during such work.

The reasons for the variability in growth are probably the great diversity of habitats occupied by the snapper and its longevity, both of which expose it to a wide range of environmental conditions.

Comparison with Previously Published Growth Rates

The growth rates published by Cassie (1955) and Longhurst (1958) were compared with the growth rates obtained in this study (Fig. 23). Both were based on smaller samples and covered fewer age groups than were considered in this study. Cassie's growth rate is faster than that from trawl-caught fish in this study, but if his curve was extended it would agree fairly well with the faster growth curve of Danish seine-caught fish. Longhurst's growth rate is also faster, particularly for older fish.

There are four possible reasons for these differences:

1. *Different interpretations of scale annuli.* Longhurst's scales and original data are on file at the Fisheries Research Division. I reread the scales from the same criteria as those adopted in this study and obtained virtually identical results to those of Longhurst, which indicated that this was not the reason for the difference.

2. *Suitability of scales used.* Many of the scales in Cassie's and Longhurst's collections were small, misshapen, and hard to read. Cassie's scales were taken mostly from "immediately behind the head and above the lateral line" (1956c, page 330), and Longhurst's scales appeared to have come from a similar area. Subsequent work (Paul 1968a) suggested that such scales would be unsuitable for age reading. Additional material collected to examine this point showed that scales from above the lateral

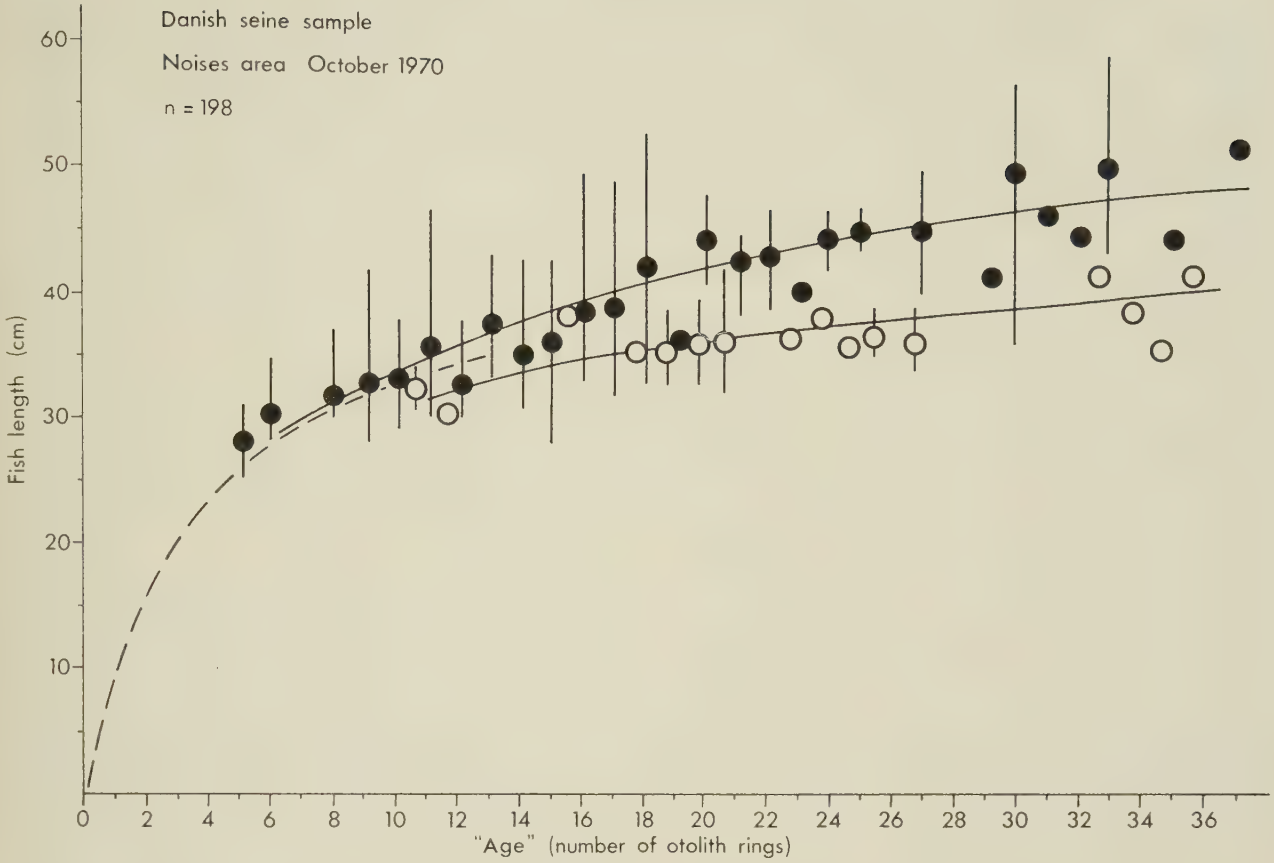

Fig. 22: Growth rate of a Hauraki Gulf snapper sample taken by Danish seining, October 1970, compared with the growth rate established from trawl-caught samples. Growth curve (dashed line) rising from origin at left: Growth rate from trawl-caught samples (Figs. 16 and 17). Growth curve through solid circles: Data from Danish seine-caught fish with good agreement between scale and otolith readings. Growth curve through open circles: Data from Danish seine-caught fish with poor agreement (more than 20% disagreement) between scale and otolith readings. Curves have been fitted by eye.

line were less easy to read, owing to crowded marginal annuli, than scales from below the line; moreover some above-line scales from fish older than 4 or 5 had fewer annuli. Thus, there is a strong probability that Cassie and Longhurst both underestimated the age of their older fish by several years.

3. *Sampling faster-growing populations.* The increased growth rate obtained by the authors referred to might have been due to their sampling only the faster-growing "populations" of Hauraki Gulf snapper. However, as their unpublished records show that their samples were obtained from the same localities as those included in the present study, where environmental conditions were presumably also similar, this possibility is unlikely.

4. *A change in growth rate with time.* There might have been a real change in the growth rate of Hauraki Gulf snapper during the time interval between the studies. Some slowing of adult growth about 1960 is suggested in this bulletin, but the data are inadequate for a proper investigation of this possibility.

Length-Weight and Age-Weight Relationships

Length-Weight Relationship. Many measurements of fork length and total weight of adult snapper taken from several regions were already on file at the Fisheries Research Division, and additional juvenile fish from the Hauraki Gulf were measured and weighed in June 1968. These were considered sufficient to establish an overall length-weight relationship.

Trial log/log plots of these data gave an essentially straight line. Calculated regressions for regional groupings are listed in Table 8. As male and female fish (Bay of Plenty sample) gave virtually identical regression equations and Cassie (1957b) had also found both sexes to be similar, the sexes were combined.

Samples of adult fish from east Northland, the Bay of Plenty, and Tasman Bay gave very similar length-

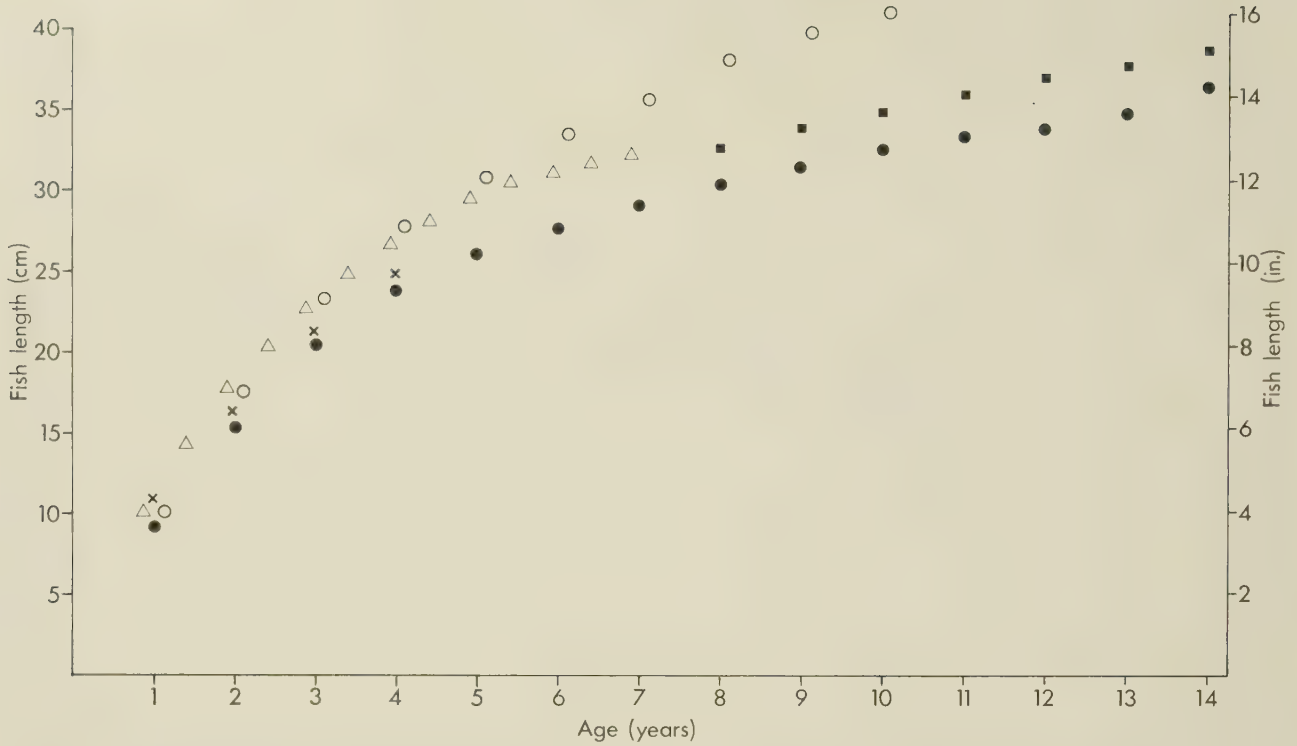

Fig. 23: Snapper growth rates determined in this study, compared with previously published growth rates. Solid circles: Mean back-calculated lengths for Kawau Island fish, from Table 2. Solid squares: Growth rate of Danish seine-caught snapper, from Fig. 22, upper curve. Crosses: Modal lengths at the end of the first 4 calendar growth years. All are from this study. Open triangles are from Cassie (1955, Table 28). Open circles are from Longhurst (1958, Fig. 5).

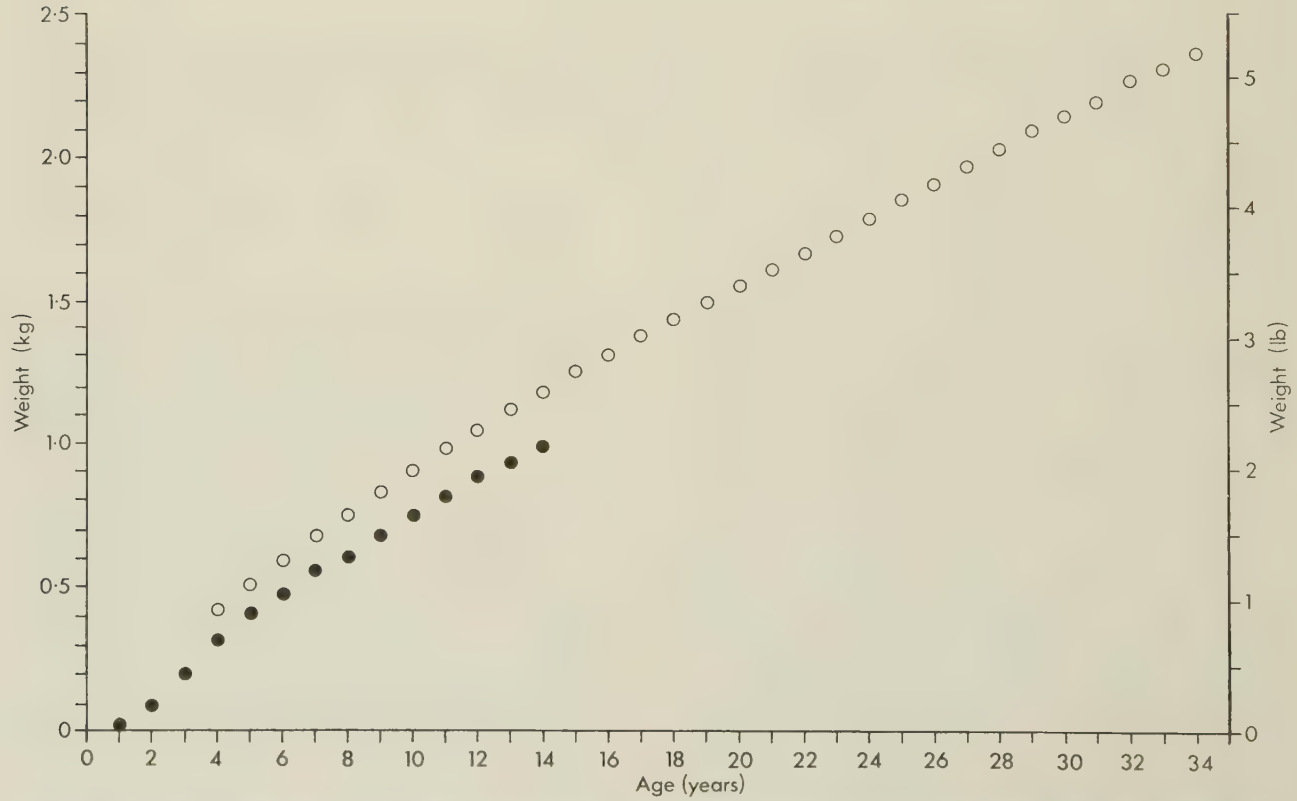

Fig. 24: Age-weight relationship of Hauraki Gulf snapper, derived from mean length-age relationship (Fig. 22) and length-weight relationship (Table 9). Solid circles: Age-weight relationship of trawl-caught snapper (Figs. 16, 17, and 22). Open circles: Age-weight relationship of faster-growing Danish seine-caught snapper (Fig. 22).

1970). The nomograph simplifies back calculation by taking into account both the curvilinear fish length-scale size relationship and the positive intercept on the fish length axis and allows the lengths of a fish at successive annuli to be determined from a single setting of a movable arm.

It was assumed that the samples of Hauraki Gulf snapper on which the nomograph was based were taken from sufficient localities to represent a "generalised" Hauraki Gulf snapper stock at the time of sampling.

Scale readings (focus to successive annulus measurements) from the February and June 1968 samples were converted to back-calculated lengths by this method, and the results were plotted in a similar way to those in Fig. 4 in Cassie (1956c) except that they were grouped by "age" rather than by fish length (Fig. 19).

Most of the lower values show good agreement with observed winter modal lengths (see Table 2).

The slope and irregularities of the higher lines clearly reflect the mean length at capture of fish in each "age" group. The fish with 11 annuli, for example, were on average larger than those with 12 annuli, and their L_n values from L_3 (=maturity) onwards were correspondingly larger. That is, fish that are large for their age back calculate larger than average L values and vice versa.

A comparison can be made between mean back-calculated lengths (mean L_1, L_2, L_3, etc.) and mean

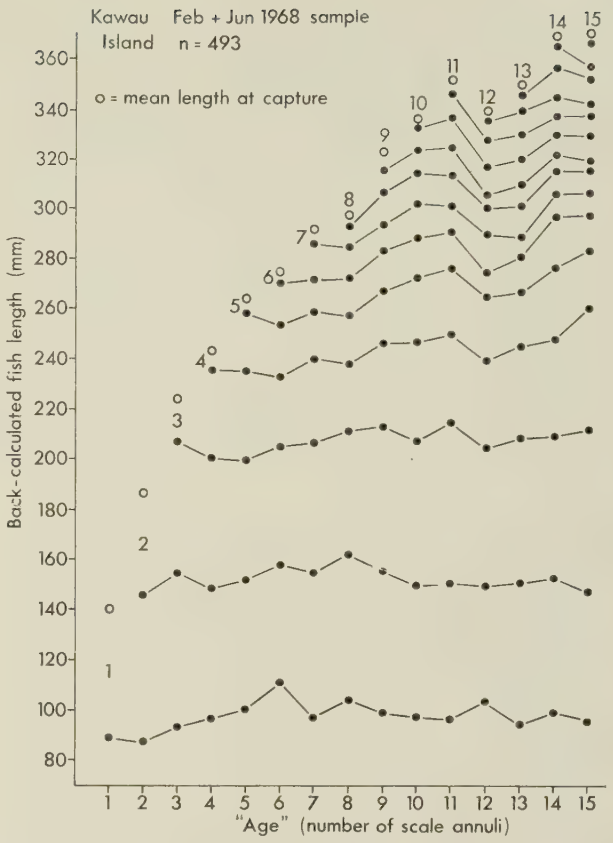

Fig. 19: Variation in back-calculated L_n values with increasing number of scale annuli (based on nomograph). Numbers of fish in each "age group" are listed in Table 2. Mean length at capture is by year class, from Table 2.

TABLE 2: Comparison of mean back-calculated lengths with measured lengths at capture, based on February and June 1968 Kawau Island samples.

Mean back-calculated length by No. of annuli*			Measured lengths at capture							Observed modal length in winter of first three ages (from Fig. 10)	
			Mean length by year class (=No. of annuli)†				Mean length by growth season‡				
No. of annuli	Mean length (mm)	No.	Year class	No. of annuli	Mean length (mm)	No.	Growth season	Mean length (mm)	No.	Growth season	Modal length (mm)
			1968§	0	98	37					
1	96	457	1967	1	140	65	1	106	68	1	95
2	152	392	1966	2	186	91	2	166	93	2	155
3	207	301	1965	3	225	47	3	218	66	3	205
4	240	254	1964	4	244	33	4	242	39	–‖	–
5	262	221	1963	5	264	39	5	258	36	–	–
6	278	182	1962	6	275	43	6	274	41	–	–
7	292	139	1961	7	291	27	7	284	30	–	–
8	303	112	1960	8	297	27	8	294	29	–	–
9	315	85	1959	9	322	18	9	310	15	–	–
10	326	67	1958	10	334	14	10	332	20	–	–
11	334	53	1957	11	351	18	11	345	13	–	–
12	337	35	1956	12	338	23	12	344	28	–	–
13	348	12	1955	13	348	8	13	352	9	–	–
14	363	4	1954	14	365	3	14	350	6	–	–
15	365	1	1953	15	365	1	15	365	1	–	–

* Means of horizontal lines in Fig. 19.

† For example, February fish with 1 annulus + June fish with 1 annulus = 1967 year class, but are separated by almost one growth season. Mean lengths are shown in Fig. 19.

‡ For example, February fish with 1 annulus + June fish with no annulus = fish approximately at end of one growth season.

§ June sample only.

‖ – indicates insufficient data.

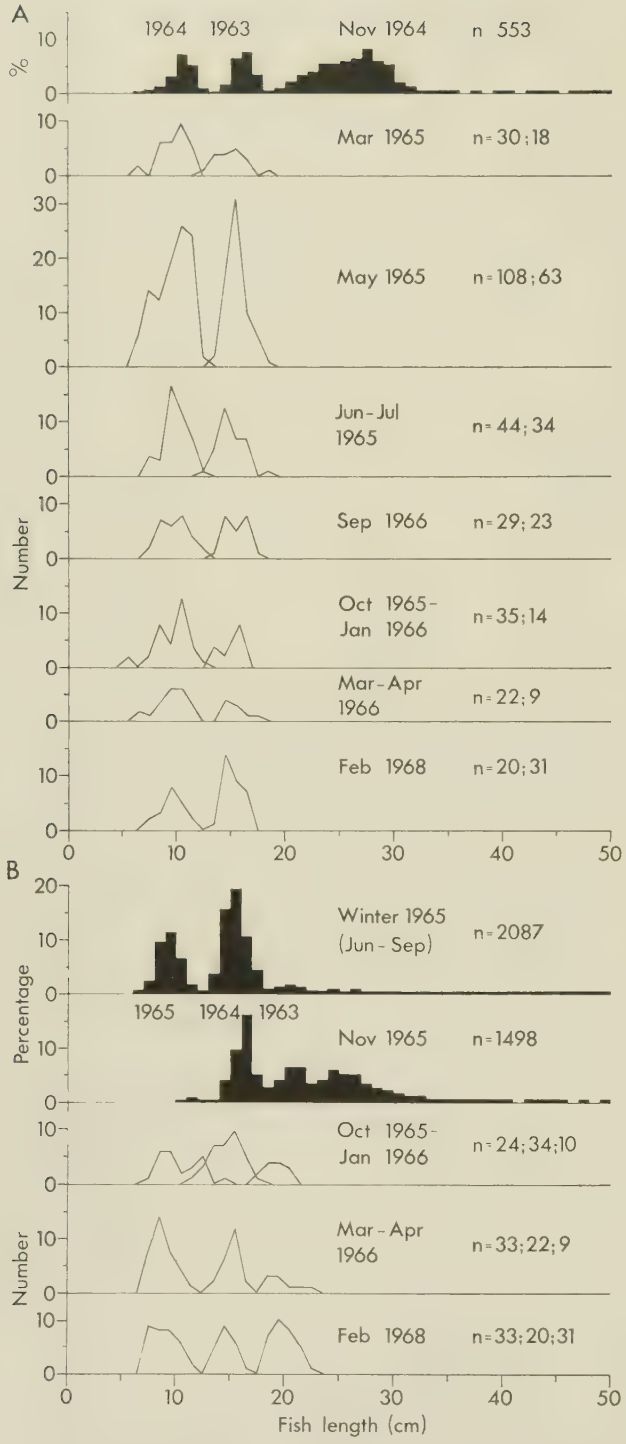

Fig. 20: Comparison of back-calculated lengths with observed lengths at (winter) annulus formation. A: Comparison of L_1 values of 1964 year class, and L_2 values of 1963 year class, with modal lengths of these year classes in spring (November) 1964 (no winter data are available; modal lengths would be slightly smaller than those in spring). B: Comparison of L_1 values of 1965 year class, L_2 values of 1964 year class, and L_3 values of 1963 year class, with modal lengths of these year classes in winter (June–September) and spring (November) 1965.

TABLE 3: Variation in growth rate of juvenile snapper at three stations in the Hauraki Gulf—Kawau Island, Mahurangi Harbour entrance, and Motuihe Channel, Motutapu Island.

	Year class			
Sampling period	1965	1964	1963	Station
1964 November	–	10.5	16.0	Kawau
	–	11.5	17.5	Motuihe
1965 May	9.0	15.0	19.5	Kawau
	9.0*	16.0	21.5	Mahurangi
	–	16.0	21.5	Motuihe
July	9.5	15.5	–	Kawau
	8.0*	16.5	–	Mahurangi
	10.5	16.0	21.5	Motuihe
September	9.5	15.5	20.5	Kawau
	10.5	17.0	22.5	Mahurangi
	9.0*	16.0	21.5	Motuihe
November	11.5	16.5	20.5	Kawau
	11.0*	17.5	22.5	Mahurangi
	12.0	17.0	22.0	Motuihe
December	–	–	20.5	Kawau
	–	–	23.0	Mahurangi
1966 January	12.5	17.0	20.5	Kawau
	–	19.0	–	Mahurangi
	14.0	–	22.5	Motuihe
March	13.5	18.5	22.0	Kawau
	14.5	20.5	24.0	Mahurangi
	15.5	21.0	24.0	Motuihe
May	15.5	–	–	Kawau
	17.0	–	–	Motuihe

Modal lengths are estimated to nearest 0.5 cm by eye from length-frequency distributions; see Fig. 10 for relationship between estimated and calculated modal lengths in the Kawau samples. In general the Mahurangi and Motuihe modal lengths are greater than those from Kawau; exceptions are marked with an asterisk.

A dash indicates insufficient fish or that the modal length of the year class is inadequately defined.

lengths at capture by (a) number of annuli and (b) number of growing seasons (Table 2). Mean back-calculated lengths are more regularly spaced than are lengths at capture, because they average out the growth history of several year classes. Lengths at capture reflect the growth rate of single year classes, which can—where sufficient data are available—be compared with the mean growth rate for the region to detect any changes in growth rate with time. Allowance must, of course, be made for the fact that lengths at capture will be greater than back-calculated lengths, because they include some fish growth after the time of annulus formation.

The back calculation technique can also be tested by back calculating L_1, L_2, etc., from single year classes at successive sampling periods and comparing the size distribution of the L_n values with the observed length-frequency distribution of the year classes at the time of annulus formation. Data from the 1963, 1964, and 1965 year classes of Hauraki Gulf snapper (Fig. 20) show good agreement between the back-calculated and observed lengths.

Back calculation of snapper growth from suitable scales can thus be regarded as reliable and can be simplified by use of a nomograph.

VARIATIONS IN GROWTH RATE

Juvenile Growth

Regional Variations in Juvenile Growth. It soon became apparent during this study that the modal size of juvenile age groups varied between localities.

At two localities in particular, Mahurangi Harbour (two stations) and Motutapu, juvenile snapper were consistently 1–2 cm larger than at Kawau Island (Table 3). The supposition that the Mahurangi and Motutapu values were greater than Kawau Island values was tested with the null hypothesis that there was no difference. Kawau Island modes equalled or were greater than Mahurangi or Motutapu modes only thrice in 35 comparisons, a probability much less than 5%; thus the observed modal growth differences were significant.

This feature was investigated further by using the nomograph to back calculate the juvenile growth rate of separate selected year classes from Kawau Island, Mahurangi Harbour entrance, and Motutapu (Table 4). (The nomograph was based on combined samples from these and other localities and would thus average out rather than create any variations in the data.) The mean values in Table 4 show that by the end of the second (growth) year the Mahurangi and Motutapu fish were 6–11 mm larger than Kawau Island fish, and by the end of the third year they were 12–18 mm larger.

Annual Variations in Juvenile Growth. During the spring, summer, and autumn of 1961–62 first-year growth of the 1962 year class and second-year growth of the 1961 year class were greater by 10–15 mm than that of adjacent year classes (Table 4). That summer in the Hauraki Gulf was one of the warmest and calmest on record (New Zealand Meteorological Service 1964) (see Fig. 36). As sea and air temperatures in the Gulf are closely related (de Lisle 1965, Paul 1968b), it is reasonable to assume that in the shallow south-west Gulf feeding and growth conditions were better than average.

Adult Growth

Regional Variations in Adult Growth. The growth rates of snapper from six localities, from Horn Rock in the outer Gulf to a shallow Firth of Thames station, were determined (Tables 5 and 6). These can be grouped into three regions: the sheltered Firth of Thames, the more open waters of the inner Gulf, and the exposed outer Gulf. Such a grouping should reveal any growth differences which were there. If the trend shown by juveniles continued, growth would be fastest in the Firth of Thames and slowest in the outer Gulf. This possibility was tested with the null hypothesis

TABLE 4: Mean juvenile growth of several year classes of snapper at three localities in the shallow south-west region of the Hauraki Gulf, based on nomograph back calculations.

Locality	Year class	Growth in 1st year (mm)	No. in sample	Growth in 2nd year (mm)	No. in sample	Growth in 3rd year (mm)	No. in sample	Growth in 4th year (mm)	No. in sample
Kawau Island and Tiritiri Matangi	1961	98	6	63	6	44	6	35	6
	1962	111	29	54	29	51	29	28	10
	1963	99	109	52	109	45	12		
	1964	98	139	50	24				
	1965	91	20						
	Mean growth*	99, 99	303	53, 55	168	49, 47	47	31, 32	16
	Mean cumulative length	99, 99		152, 154		201, 201		232, 233	
Mahurangi Harbour entrance	1961	89	15	76	15	57	15	30	15
	1962	113	19	61	19	50	19	26	1
	1963	94	11	67	11	53	5		
	1964	89	50	60	6				
	1965	86	12						
	Mean growth	93, 94	107	67, 66	51	53, 53	39	30, 28	16
	Mean cumulative length	93, 94		160, 160		213, 213		242, 241	
Motuihe Channel, Motutapu Island	1961	–†	–	–	–	–	–	–	–
	1962	116	14	49	14	54	14	–	–
	1963	103	28	58	28	54	11		
	1964	101	32	67	2				
	1965	107	3						
	Mean growth	105, 107	77	56, 58	44	54, 54	25		
	Mean cumulative length	105, 107		161, 165		215, 219			

* Weighted mean and simple mean of combined year classes are given in that order; mean cumulative lengths are similarly arranged.

† – indicates insufficient data.

TABLE 5: Variation in growth rate, from age at capture, of adult Hauraki Gulf snapper.

LOCALITIES

Age (years)	Firth Length (cm)* Mean	Range	Lake Length (cm) Mean	Range	Mahurangi Hr entrance† Length (cm) Mean	Range	Waiheke-Coromandel Length (cm) Mean	Range	Kawau Island Length (cm) Mean	Range	Horn Rock Length (cm) Mean	Range
3	24.9	20–27 (25)‡	–§	–	21.3	20–21 (5)	21.9	18–25 (48)	22.0	18–24 (44)	21.3	18–24 (41)
4	27.9	26–29 (11)	–	–	25.1	23–26 (17)	25.4	23–27 (22)	24.5	21–26 (18)	23.7	21–25 (13)
5	29.5	27–31 (8)	–	–	27.5	26–28 (7)	28.0	26–29 (16)	26.8	24–28 (15)	25.7	23–27 (6)
6	31.0	28–34 (8)	28.2	26–29 (3)	28.5	26–29 (11)	28.4	26–30 (8)	27.9	26–30 (13)	27.2	24–29 (6)
7	32.3	30–37 (23)	30.1	28–32 (20)	30.0	28–31 (6)	28.9	26–31 (13)	29.4	27–32 (17)	27.9	25–32 (18)
8	34.4	32–38 (12)	31.0	29–33 (8)	30.0	28–32 (6)	30.1	27–33 (13)	30.1	27–32 (12)	28.7	25–33 (19)
9	35.5	32–38 (13)	32.4	28–36 (16)	32.5	30–33 (5)	32.0	28–34 (10)	30.6	28–32 (6)	31.5	29–34 (15)
10	35.5	35 (1)	32.0	31–33 (4)	35.0	33–39 (6)	31.5	28–34 (2)	34.0	33–34 (2)	32.0	29–34 (8)

REGIONS

Age (years)	Firth of Thames Length (cm) Mean	Range	Inner Gulf Length (cm) Mean	Range	Outer Gulf Length (cm) Mean	Range
3	24.9	20–27 (25)	21.9	18–25 (97)	21.3	18–24 (41)
4	27.9	26–29 (11)	25.0	21–27 (57)	23.7	21–25 (13)
5	29.5	27–31 (8)	27.2	24–29 (28)	25.7	23–27 (6)
6	30.2	28–34 (11)	28.2	26–30 (32)	27.2	24–29 (6)
7	31.3	28–37 (43)	29.3	26–32 (36)	27.9	25–32 (18)
8	33.0	29–38 (20)	30.1	27–33 (31)	28.7	25–33 (19)
9	33.9	28–38 (29)	31.7	28–33 (21)	31.5	29–34 (15)
10	32.7	31–35 (5)	34.1	28–39 (10)	32.0	29–34 (8)

* Range given as original measurements; 0.5 cm added in calculation of mean.
† Mahurangi sample taken in June 1965; all other samples collected in January 1969.
‡ Numbers at each age in parentheses.
§ – indicates no data.

TABLE 6: Variation in growth rate of adult snapper collected in the Hauraki Gulf in January 1969, shown by mean and range of lengths of the 1962 year class, which have been calculated from scale reading and nomograph.

LOCALITIES

L_n*	Firth Length (cm)† Mean	Range	Lake Length (cm) Mean	Range	Waiheke-Coromandel Length (cm) Mean	Range	Kawau Island Length (cm) Mean	Range	Horn Rock Length (cm) Mean	Range
L_3	21.9	18–26	21.6	17–25	21.7	20–23	21.5	18–25	20.7	18–24
L_4	27.1	22–29	24.9	21–29	24.5	21–26	24.6	22–27	23.1	20–26
L_5	29.8	25–33	27.6	25–30	26.6	24–28	26.5	24–29	25.1	22–29
L_6	31.3	27–35	29.0	27–31	27.8	25–29	27.9	25–31	26.6	24–30
L	32.7	30–37	30.1	28–32	28.8	26–31	29.4	27–32	27.9	25–32
	No.=19		No.=20		No.=12		No.=17		No.=18	

REGIONS

L_n*	Firth of Thames Length (cm) Mean	Range	Inner Gulf Length (cm) Mean	Range	Outer Gulf Length (cm) Mean	Range
L_3	22.2	17–26	21.6	18–25	20.7	18–24
L_4	26.0	21–29	24.6	21–27	23.1	20–26
L_5	28.7	25–33	26.6	24–29	25.1	22–29
L_6	30.1	27–35	27.9	25–31	26.6	24–30
L	31.4	28–37	29.2	26–32	27.9	25–32
	No.=39		No.=29		No.=18	

* Back-calculated lengths at scale annuli 3–6.
† Range given as original measurements; 0.5 cm added in nomograph back calculations.

that there was no significant difference in mean growth rate between the three regions. Then the probability of observing the arrangement that Firth growth is greater than inner Gulf growth and inner Gulf growth is greater than outer Gulf growth at any age is 1/8. At the 5% significance level there must be four deviations from this pattern for eight sets of observations and two for five sets. In fact, there was one in eight sets (Table 5) and nil in five sets (Table 6); thus the hypothesis is rejected and a real difference in growth assumed.

There is not a simple relationship between adult growth rate and depth; Kawau Island and Mahurangi Harbour fish were taken from different depths, but had similar growth rates. Presumably the fish in the inner Gulf move freely between the open Gulf waters and the shallow marginal feeding grounds. However, the higher growth rate observed in Firth of Thames snapper suggests that these fish may comprise a stock which remains reasonably distinct from snapper in the inner and outer Gulf.

These differences in growth are small, apply to means rather than to individual fish (which show a considerable range of growth rates), and are most obvious in Firth of Thames fish. Most snapper available to the commercial trawl and Danish seine fishery inhabit open water and would have a mean growth rate similar to that described for inner and outer Gulf snapper in Tables 5 and 6.

Several of the scales from large fish in the samples discussed above had crowded annuli near the scale edge (Table 7), similar to those previously found (page 30) to give underestimates of age. There was a greater proportion of these from Firth of Thames stations.

Comparison of scale and otolith readings from a subsequent sample collected at the Firth of Thames entrance (Lake locality) showed that almost all fish 12 years and older had scale and otolith ring counts which differed greatly from each other (Fig. 21). This characteristic has been assumed (page 30) to represent periods of little or no growth. At first sight this appears to conflict with the finding that growth up to age 10 is more rapid in the Firth than at other localities. However, in terms of fish size, population structure, and apparent abundance Firth snapper differ from those of the rest of the Hauraki Gulf (unpublished data); further work to clarify these differences is needed before a definitive statement on the growth rate of Firth snapper can be made.

TABLE 7: Numbers of older snapper (12 or more otolith rings) at several Hauraki Gulf stations, January 1969, with discrepancies of two rings or more between scale and otolith readings.

Station	Total No. in sample	No. of older fish (12 or more otolith rings)	Fish with ring count discrepancies (% of older fish)
Horn Rock	267	62	1.6
Kawau Island	219	29	20.6
Firth	138	21	23.8
Waiheke-Coromandel	201	27	51.7
Lake	136	73	91.8
Lake (March–April 1970)	118	28	85.7

Further evidence of growth rate variation in adult Hauraki Gulf snapper is shown by the age determinations (otolith ring count) of 198 snapper caught by Danish seining in the inner Gulf during the spawning season (Fig. 22). There is a wide spread of ages at each length; a 30-cm fish could be from 5 to 15 years old and a 35-cm fish from 8 to 34. In this sample many fish older than 10 also showed differences between scale and otolith readings, the criterion used above for slow-growing ("stunted") fish. These fish, defined in this particular sample by an otolith-scale reading difference of more than 20% and identified separately in Fig. 22, do in fact have a slower growth rate than the other fish.

In the original data there was also some evidence of a bimodal length distribution at ages 9–11. The smaller modes coincided with the growth curve previously established for Kawau Island fish. The larger modes represent faster-growing fish whose origin is unknown; they may be fast-growing Firth of Thames fish which moved out into the Gulf to spawn or they may be fish from an area outside the Hauraki Gulf which moved in to spawn.

Annual Variations in Adult Growth. The differences between scale and otolith ring counts suggest that adult growth may decline or cease for some years at certain localities. Differences between back-calculated mean lengths and mean lengths at capture (Table 2) could also be used to give evidence of this.

General Features of Snapper Growth

Although geographical and temporal variations in the growth rate of snapper have been demonstrated, all the available evidence (page 35, unpublished data, Vooren and Coombs in press) suggests that the growth rate of fish taken by trawl near Kawau Island is representative of the snapper on the main Hauraki Gulf trawling and Danish seining grounds. Nevertheless, because variations do occur, the growth section in this paper does not conclude with quantitative growth equations and parameters which can be used as a basis for subsequent work on recruitment, yields,

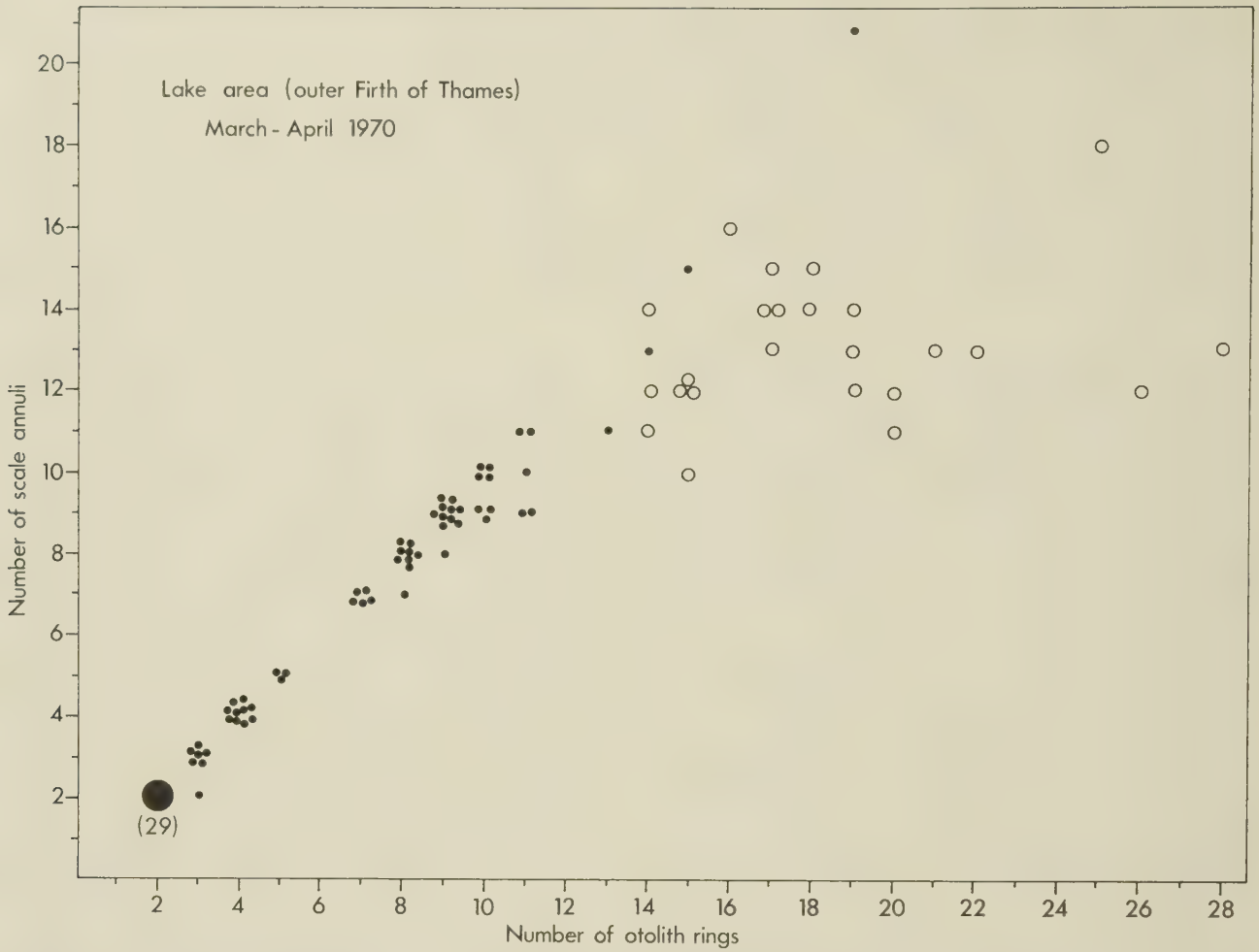

Fig. 21: Comparison of scale and otolith age readings from snapper caught at the Lake locality, March–April 1970. Solid circles: Scales subjectively judged to be "normal"; n=90. Open circles: Scales subjectively judged to have an incomplete series of annuli; n=24.

and mortalities. These must be calculated directly from appropriate samples obtained during such work.

The reasons for the variability in growth are probably the great diversity of habitats occupied by the snapper and its longevity, both of which expose it to a wide range of environmental conditions.

Comparison with Previously Published Growth Rates

The growth rates published by Cassie (1955) and Longhurst (1958) were compared with the growth rates obtained in this study (Fig. 23). Both were based on smaller samples and covered fewer age groups than were considered in this study. Cassie's growth rate is faster than that from trawl-caught fish in this study, but if his curve was extended it would agree fairly well with the faster growth curve of Danish seine-caught fish. Longhurst's growth rate is also faster, particularly for older fish.

There are four possible reasons for these differences:

1. *Different interpretations of scale annuli.* Longhurst's scales and original data are on file at the Fisheries Research Division. I reread the scales from the same criteria as those adopted in this study and obtained virtually identical results to those of Longhurst, which indicated that this was not the reason for the difference.
2. *Suitability of scales used.* Many of the scales in Cassie's and Longhurst's collections were small, misshapen, and hard to read. Cassie's scales were taken mostly from "immediately behind the head and above the lateral line" (1956c, page 330), and Longhurst's scales appeared to have come from a similar area. Subsequent work (Paul 1968a) suggested that such scales would be unsuitable for age reading. Additional material collected to examine this point showed that scales from above the lateral

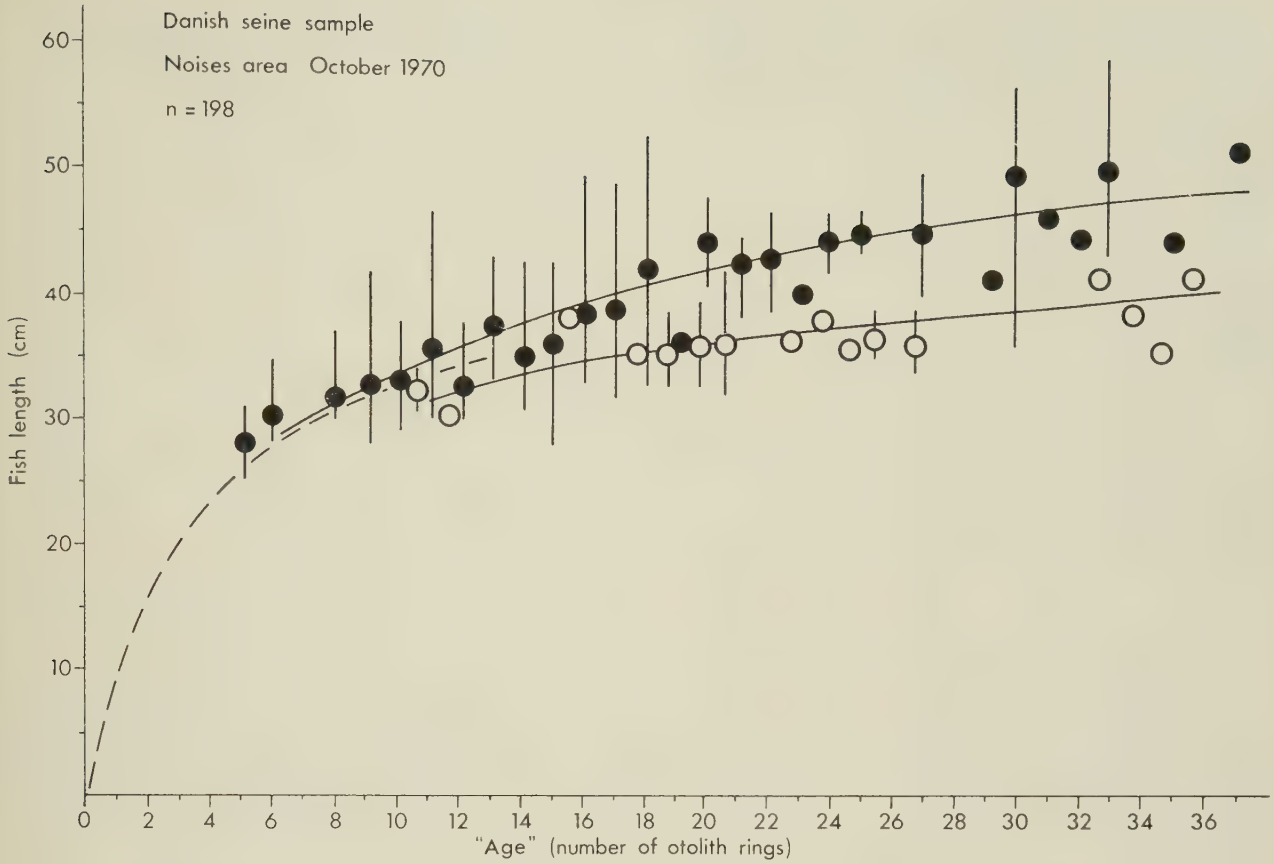

Fig. 22: Growth rate of a Hauraki Gulf snapper sample taken by Danish seining, October 1970, compared with the growth rate established from trawl-caught samples. Growth curve (dashed line) rising from origin at left: Growth rate from trawl-caught samples (Figs. 16 and 17). Growth curve through solid circles: Data from Danish seine-caught fish with good agreement between scale and otolith readings. Growth curve through open circles: Data from Danish seine-caught fish with poor agreement (more than 20% disagreement) between scale and otolith readings. Curves have been fitted by eye.

line were less easy to read, owing to crowded marginal annuli, than scales from below the line; moreover some above-line scales from fish older than 4 or 5 had fewer annuli. Thus, there is a strong probability that Cassie and Longhurst both underestimated the age of their older fish by several years.

3. *Sampling faster-growing populations.* The increased growth rate obtained by the authors referred to might have been due to their sampling only the faster-growing "populations" of Hauraki Gulf snapper. However, as their unpublished records show that their samples were obtained from the same localities as those included in the present study, where environmental conditions were presumably also similar, this possibility is unlikely.

4. *A change in growth rate with time.* There might have been a real change in the growth rate of Hauraki Gulf snapper during the time interval between the studies. Some slowing of adult growth about 1960 is suggested in this bulletin, but the data are inadequate for a proper investigation of this possibility.

Length-Weight and Age-Weight Relationships

Length-Weight Relationship. Many measurements of fork length and total weight of adult snapper taken from several regions were already on file at the Fisheries Research Division, and additional juvenile fish from the Hauraki Gulf were measured and weighed in June 1968. These were considered sufficient to establish an overall length-weight relationship.

Trial log/log plots of these data gave an essentially straight line. Calculated regressions for regional groupings are listed in Table 8. As male and female fish (Bay of Plenty sample) gave virtually identical regression equations and Cassie (1957b) had also found both sexes to be similar, the sexes were combined.

Samples of adult fish from east Northland, the Bay of Plenty, and Tasman Bay gave very similar length-

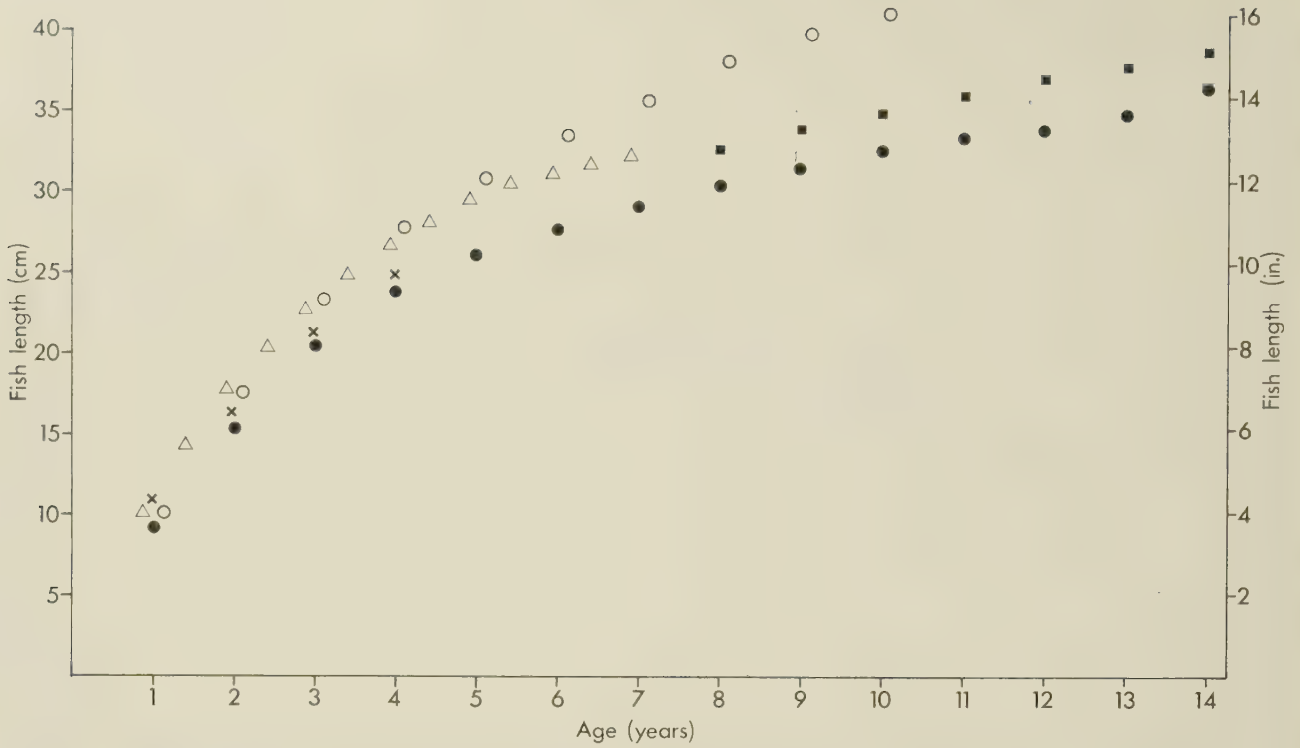

Fig. 23: Snapper growth rates determined in this study, compared with previously published growth rates. Solid circles: Mean back-calculated lengths for Kawau Island fish, from Table 2. Solid squares: Growth rate of Danish seine-caught snapper, from Fig. 22, upper curve. Crosses: Modal lengths at the end of the first 4 calendar growth years. All are from this study. Open triangles are from Cassie (1955, Table 28). Open circles are from Longhurst (1958, Fig. 5).

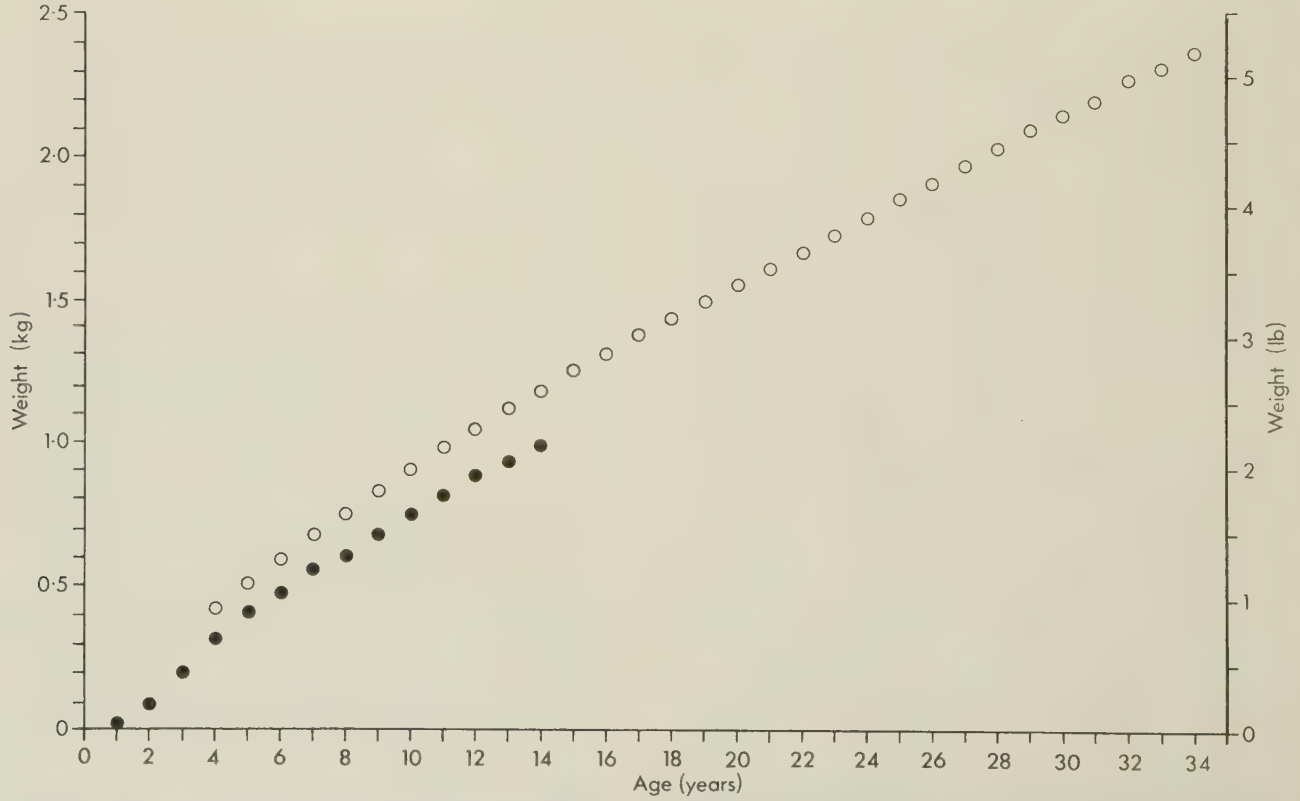

Fig. 24: Age-weight relationship of Hauraki Gulf snapper, derived from mean length-age relationship (Fig. 22) and length-weight relationship (Table 9). Solid circles: Age-weight relationship of trawl-caught snapper (Figs. 16, 17, and 22). Open circles: Age-weight relationship of faster-growing Danish seine-caught snapper (Fig. 22).

TABLE 8: Length-weight relationships of New Zealand snapper (length in cm, weight in lb, as originally recorded).

Locality	Size range (cm)	No.	Regression
East Northland	25–67	253	$\log W = 2.9057 \log L - 4.1877$
Hauraki Gulf	8–28	242	$\log W = 2.5595 \log L - 3.7082$
Bay of Plenty	19–57	201	$\log W = 2.9240 \log L - 4.2069$
	Males:		$\log W = 2.9263 \log L - 4.2082$
	Females:		$\log W = 2.9240 \log L - 4.2058$
Tasman Bay	29–71	84	$\log W = 2.8931 \log L - 4.1486$
Combined	8–71	780	$\log W = 2.7931 \log L - 4.0069$

weight regressions (Table 8). A sample of juvenile Hauraki Gulf fish was slightly different, but still sufficiently similar to be grouped with the others. The combined data gave the length-weight relationship:

$$\log_{10} W = 2.793 \log L - 4.007 \text{ (cm, lb)}$$
or $$\log_{10} W = 2.793 \log L - 4.35 \text{ (cm, kg)}$$

For ease of reference the increase of fish weight with length from these combined data is given in Table 9.

Age-Weight Relationship. Only a generalised age-weight relationship (Fig. 24) was obtained in this study. The most rapid growth in weight occurs between the ages of 2 and 5, when about 100 g is added per year. In later years growth in weight is almost linear, about 65 g being added per year.

Extrapolation of this growth curve to larger snapper, 40–60 cm in length and 7–20 kg in weight, suggests surprisingly high ages (30–60 years) for these fish. Several snapper of these ages were found, but such fish were fairly uncommon in the Hauraki Gulf trawl and Danish seine fishery (see Figs. 28–34). They may have formed a greater proportion of the commercial long line catch, which was not examined during this study, but is generally believed by fishermen to contain relatively more large fish than trawl or Danish seine catches. The larger size of line-caught snapper is in fact apparent in a series of samples measured in 1927–29 (see Fig. 27). Such larger fish are now more common in other geographical areas away from the Hauraki Gulf, particularly on the west coast of the North Island.

TABLE 9: Increase of weight with length in the New Zealand snapper, based on the equations: $\log W = 2.793 \log L - 4.007$ (length in cm, weight in lb, from original data), $\log W = 2.793 \log L - 4.35$ (length in cm, weight in kg, derived from original equation).

Length (cm)	Weight (lb)	Weight (kg)	Length (cm)	Weight (lb)	Weight (kg)
10	0.06	0.03	41	3.14	1.43
11	0.08	0.04	42	3.36	1.53
12	0.10	0.05	43	3.59	1.63
13	0.13	0.06	44	3.83	1.74
14	0.16	0.07	45	4.08	1.86
15	0.19	0.09	46	4.34	1.98
16	0.23	0.10	47	4.61	2.10
17	0.27	0.12	48	4.89	2.22
18	0.32	0.15	49	5.18	2.35
19	0.37	0.20	50	5.48	2.49
20	0.43	0.20	51	5.79	2.63
21	0.49	0.22	52	6.11	2.78
22	0.56	0.25	53	6.45	2.93
23	0.63	0.28	54	6.79	3.09
24	0.71	0.32	55	7.15	3.25
25	0.79	0.36	56	7.52	3.42
26	0.88	0.40	57	7.90	3.59
27	0.98	0.45	58	8.29	3.76
28	1.09	0.50	59	8.69	3.94
29	1.20	0.55	60	9.12	4.13
30	1.32	0.60	61	9.54	4.32
31	1.44	0.65	62	9.98	4.52
32	1.57	0.71	63	10.44	4.73
33	1.71	0.78	64	10.91	4.95
34	1.86	0.85	65	11.40	5.17
35	2.02	0.92	66	11.90	5.40
36	2.19	0.99	67	12.41	5.64
37	2.36	1.07	68	12.93	5.88
38	2.54	1.16	69	13.47	6.12
39	2.73	1.24	70	14.02	6.36
40	2.93	1.33			

DISTRIBUTION, ABUNDANCE, AND SEASONAL MIGRATIONS

The snapper is the most common and widespread species of demersal fish in the Hauraki Gulf. It was taken at most trawl stations in this study, at depths of from 4 to 155 m, but the numerical catch per hour—the measurement on which the following account of distribution and abundance is based—varied rather widely, presumably with varying environmental conditions (weather and sea conditions, time of day, tide, and the like) and with the behaviour of the fish. Nevertheless, sufficient stations were worked during each sampling period to show general trends in regional and seasonal patterns of distribution and abundance.

The age composition of fish from 2 to 24 cm in each sample was determined primarily by inspection of the length-frequency modes, plus scale reading of subsamples where modes were not conspicuous. They comprised age groups 0+ to 3+, with some small 4+ fish. Mature, adult fish, over 25 cm (and the legal size limit of 10 in.), were grouped, though a wide range of age groups was involved.

Figure 25 shows the distribution of the first four age groups of snapper—several year classes combined—in the Hauraki Gulf in 1964–66 at 6-monthly (summer and winter) intervals.

Figure 26 shows the numerical seasonal abundance of adult and juvenile snapper (the latter separated into age groups and year classes) at Kawau Island—the in-shore station for which most data are available—and at a combined group of adjacent off-shore stations (25–65 m).

As explained below (page 45) the apparent increase in abundance with age can be partly explained by escape of smaller fish through the net mesh, but is presumably also due to a gradual movement of juveniles on to trawlable grounds.

0+ AGE GROUP

This age group was observed to grow to 9–10 cm in mean length by the end of autumn (May–June), cease growth in winter, then resume growth in spring (October–November) to reach 11–12 cm at the end of the year (Fig. 10).

The smallest fish in this age group, 2–4 cm long, were taken by beach seining with a fine-mesh net in the shallow harbours and bays of the south-west Gulf in February and March 1966. Both here and in the adjacent (but west coast) Manukau Harbour they occurred in several habitats, from very turbid water in muddy tidal creeks and bays, particularly near rock or boulder outcrops or eelgrass (*Zostera*) beds, to relatively clear coastal water above gravel and weed beds at headlands and near-shore islands. They appeared to be relatively more common in the shallow harbours, but they were never taken in large numbers at any locality, though the small net used fished well and caught plentiful quantities of other fishes. Skin divers report seeing only occasional individuals or small schools of juvenile snapper among the rocks and weeds of the sea floor down to 50 m.

In March and April 1966 (late summer and early autumn) the earliest occurrence of 5–10 cm snapper in trawl catches was at the shallowest in-shore stations (5–20 m) in the south-west Gulf. In mid-autumn (May of both 1965 and 1966) considerable numbers of 5–12 cm snapper were trawled over a wider area, extending out to 40 m (Fig. 25) and approximating the area recognised by fishermen as "spawning grounds", but they were still most abundant in shore.

This distribution pattern coincides with the region of Gulf coastline comprising shallow and sheltered bays, harbours, and river mouths rather than a rocky shore line. It is supporting, though circumstantial, evidence that these habitats comprise the first-summer nursery grounds of juvenile snapper and that the autumn appearance of small juveniles on adjacent off-shore grounds represents a short seaward movement as in-shore water temperatures fall, rather than a descent from mid water as a temperature inversion (Paul 1968b) develops. However, more extensive sampling in mid water near the spawning grounds, and in very shallow water close in shore, will be necessary to locate the habitat of the smallest 0+ snapper.

1+ AGE GROUP

This age group was observed to grow from 11 to 12 cm mean length in January, stay at 15 cm during winter, and reach 16–17 cm in December (Fig. 10).

These 1+ fish were widely distributed throughout the Gulf and were most abundant in the shallow south-western area in both summer and winter (Fig. 25). Their scarcity in the Firth of Thames in winter may have indicated a movement out of this shallow area when water temperatures were low.

During this study more 1+ fish were caught at all stations than were 0+ fish (Fig. 26). The possibility that this was due to variations in year class strength is minimised by the combination of more than one year class in the data. Some of this is obviously due to a

Fig. 25: Distribution and abundance of juvenile and young adult snapper in the Hauraki Gulf, 1964–66. Several year classes have been combined in the interpretation of each age group. Sizes listed are modal lengths.

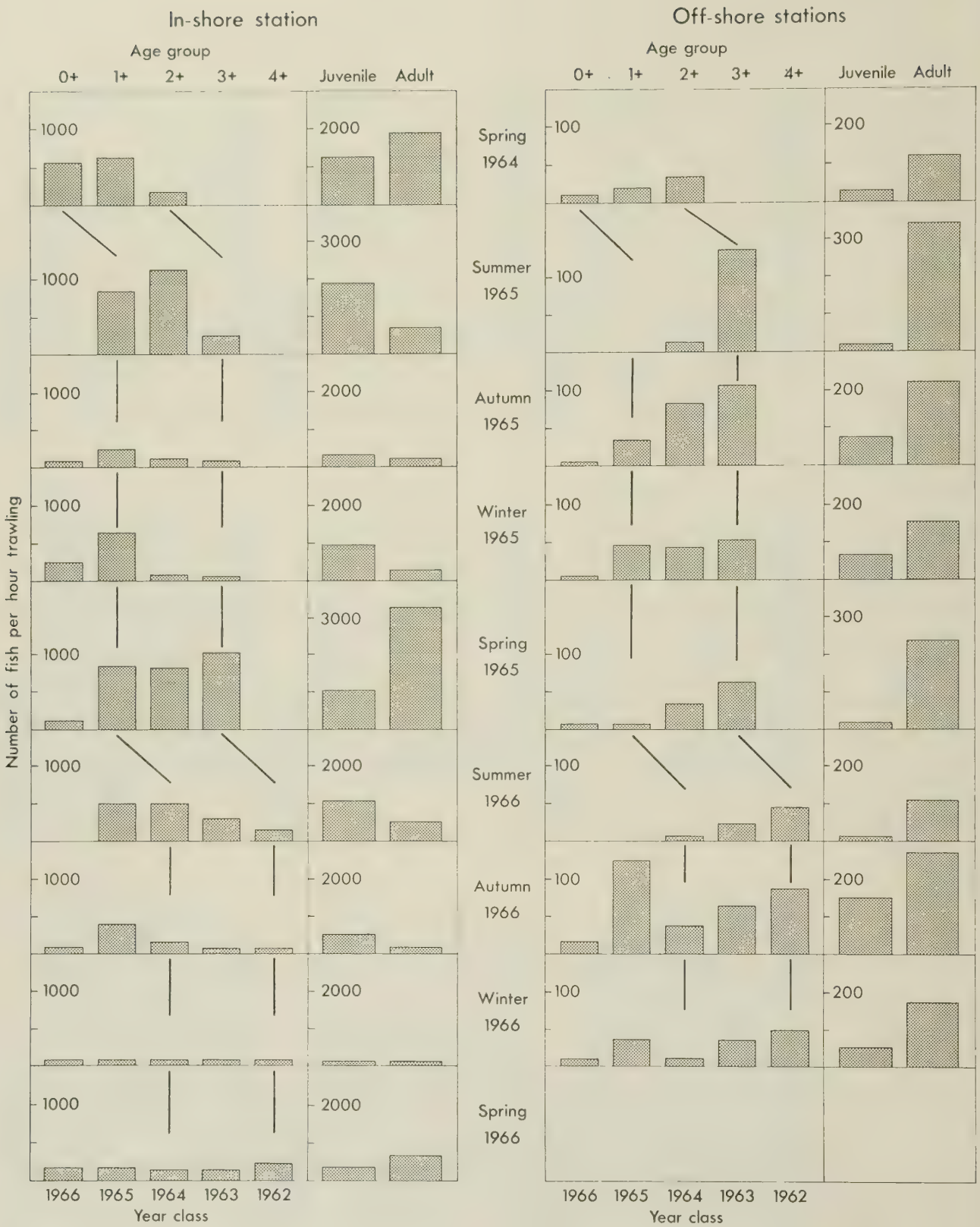

Fig. 26: Snapper abundance at an in-shore station (Kawau Island, 20–25 m) and at off-shore stations (Nos. 8, 10, 11, 25, 29, 30, 31, and 35 in Fig. 2; 25–65 m). Juvenile snapper (less than 20 cm) comprise 0+, 1+, and 2+ fish.

greater escape of the smaller fish through 3.8-cm ($1\frac{1}{2}$-in.) cod-end mesh; an extrapolation of Fig. 34 in Cassie (1955) shows that there would be a theoretical 20–40% escape of 10-cm (0+) snapper, against no escape of 15-cm (1+) fish. However, over twice as many 1+ as 0+ fish were caught at Kawau Island, and over six times as many at the combined off-shore stations (Fig. 26), which indicates that there was a steady movement of these small fish on to the clear-bottom trawling grounds from some other habitat—either the shallow bays and estuaries or the mid-water environment mentioned above.

The greatest abundance of 1+ fish during the study period was in the shallow south-west Gulf.

2+ AGE GROUP

This age group was observed to grow from 16–17 cm mean length to 21 cm in a calendar year.

Figure 25 shows the continuing spread of juvenile snapper across the Gulf from the apparent centre of abundance in the south-west.

A few of the larger fish of this age group had apparently mature, though fairly small, gonads. Their contribution to the main spawning may have been slight, but they participated in the presumed seasonal migrations of spawning fish from in shore to off shore. At the in-shore station of Kawau Island the 2+ fish were more abundant in spring and summer than in autumn and winter (Figs. 9 and 26), whereas at the combined off-shore stations (Fig. 26) the reverse was true.

3+ AGE GROUP

These fish were observed to grow from 21 cm mean length to about 25 cm in a calendar year.

They were widely distributed throughout the Gulf and like the 2+ fish were more abundant in shore in summer and off shore in winter.

4+ AGE GROUP

This age group continued the seasonal in-shore and off-shore movements of the two younger age groups (1966 data in Fig. 26) and showed some concentration in the western Gulf in summer (Fig. 25).

JUVENILE FISH

Juveniles were generally more abundant at the in-shore station, where they predominated over adults in all seasons except spring (Fig. 26). Their decline in numbers in autumn and winter corresponded to an increase in numbers at the off-shore stations, which suggests an off-shore winter migration of at least some of these fish.

ADULT FISH

Snapper over 20 cm in length were generally more abundant at the off-shore station, where there was no clear indication of any seasonal change in abundance (Fig. 26). At the in-shore station, however, there was good evidence for an influx of adult fish, 25–35 cm in length, in spring and early summer (Figs. 9 and 26). The absence of a corresponding decline in fish at the off-shore stations suggests that the spring and early summer concentrations of spawning snapper in the south-western (and probably also the south-eastern) Gulf are drawn not from the central Gulf, but from a wider area beyond that adequately sampled during this study.

Some indications of seasonal migrations of adult fish can be shown in the commercial landing statistics for Hauraki Gulf snapper (Paul 1974, in press), but these are difficult to interpret because of various economic factors also influencing the landings.

SNAPPER MOVEMENTS SHOWN BY TAGGING EXPERIMENTS

Previous tagging experiments on the snapper have not generally been successful (Paul 1967), and only small tagging projects have been done since then. The general conclusions reached from all tagging work so far are that some parts of the Hauraki Gulf snapper population are resident, that some fish may migrate seasonally but return to the same locality, and that some fish may undergo migrations of over 60 km. However, a large-scale tagging programme on trawled open-water snapper will be necessary before any clear pattern of movement (if such exists) can be established.

POPULATION STRUCTURE

PREVIOUS WORK

Hefford (1929) made the first assessment of the size structure and possible age structure of Hauraki Gulf snapper. His length-frequency data for fish caught by the four main fishing methods (trawl, Danish seine, long line, and set net) have been replotted in Fig. 27. Each size distribution was slightly different, but all were unimodal, with the mode between 30 and 35 cm; the most obvious features were that the trawl-caught fish were on average slightly larger than those caught by Danish seine, that line-caught fish were slightly larger again, and that fish caught by set net covered a smaller range of sizes, possibly because of mesh selection. Hefford provided no information on localities, mesh sizes, whether or not small fish had been discarded before sampling, or the sampling methods themselves; so his data can be used to show only the general size distribution of snapper landed into the Auckland markets at that time. Hefford (1929, page 37) commented: "Taking the results as a whole, we see that the bulk of the catches consists of medium-sized snapper, the age of which would appear to be not less than three years and not more than four or five years. The graphs are, in fact, typical of a fairly intensively fished ground, in that they show that relatively young individuals are providing the bulk of the produce." His comments on the age composition, however, appear to be based on a superficial examination of polymodal length-frequency data, because on the same page he states: "There is no means at present of ascertaining the age of snapper, but data obtained by the measurement of large numbers of fish provide material for an approximate indication as to age, and thus records of the lengths of the fish comprising a representative sample afford in practice a useful method of showing the relative age composition of the sample." His values of 3 to 5 years considerably underestimated the true position.

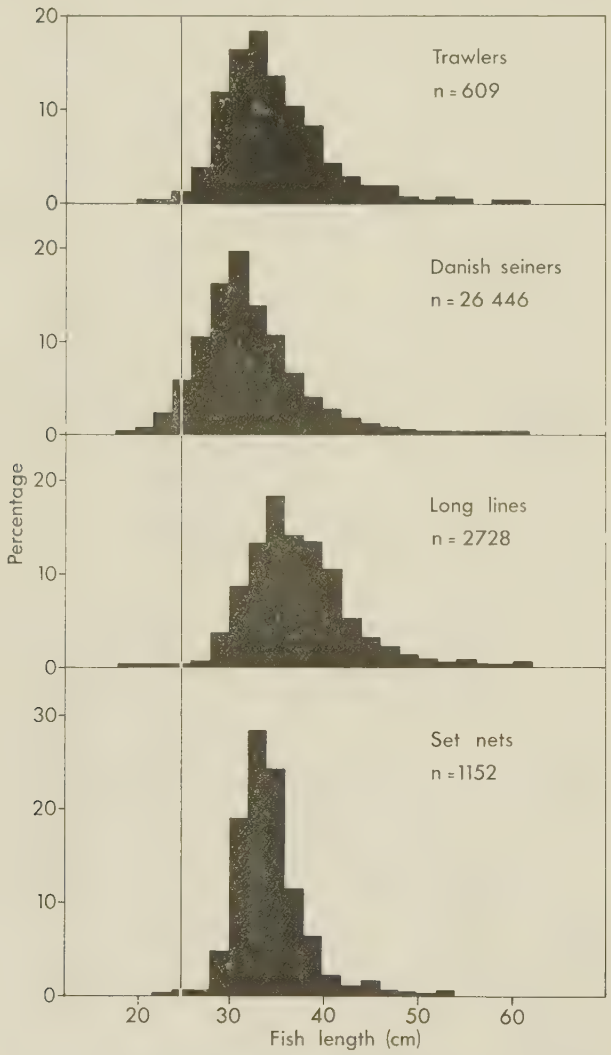

Fig. 27: Length-frequency distributions of samples taken from commercial snapper catches in the Hauraki Gulf, 1927–29. The vertical line is generalised at 25 cm, approximately equivalent to the legal size limit of 10 in. Data are from Hefford (1929, Table 7); the original measurements in centimetres have been grouped into 2-cm units.

Cassie (1955) did not specifically comment on population structure, but his Figs. 25 and 26, which show the size distribution of snapper that were caught during the studies on escape and which were plotted beside the average growth rate, do imply that a considerable proportion of the catch was over 5 years old.

It is noteworthy that Longhurst (1958), after comparing his and Hefford's data, commented that (page 492) " . . . there is no indication that significantly larger fish were being taken in this area thirty years ago".

PRESENT STUDY

Age determinations obtained during the present study were considered sufficiently reliable to allow conversion of some length-frequency data into age-frequency distributions. The variability of growth rates even within the Hauraki Gulf, and the possibility that several different populations or stocks of snapper exist (page 35), precludes the use of generalised age-length keys. The use of such keys must be

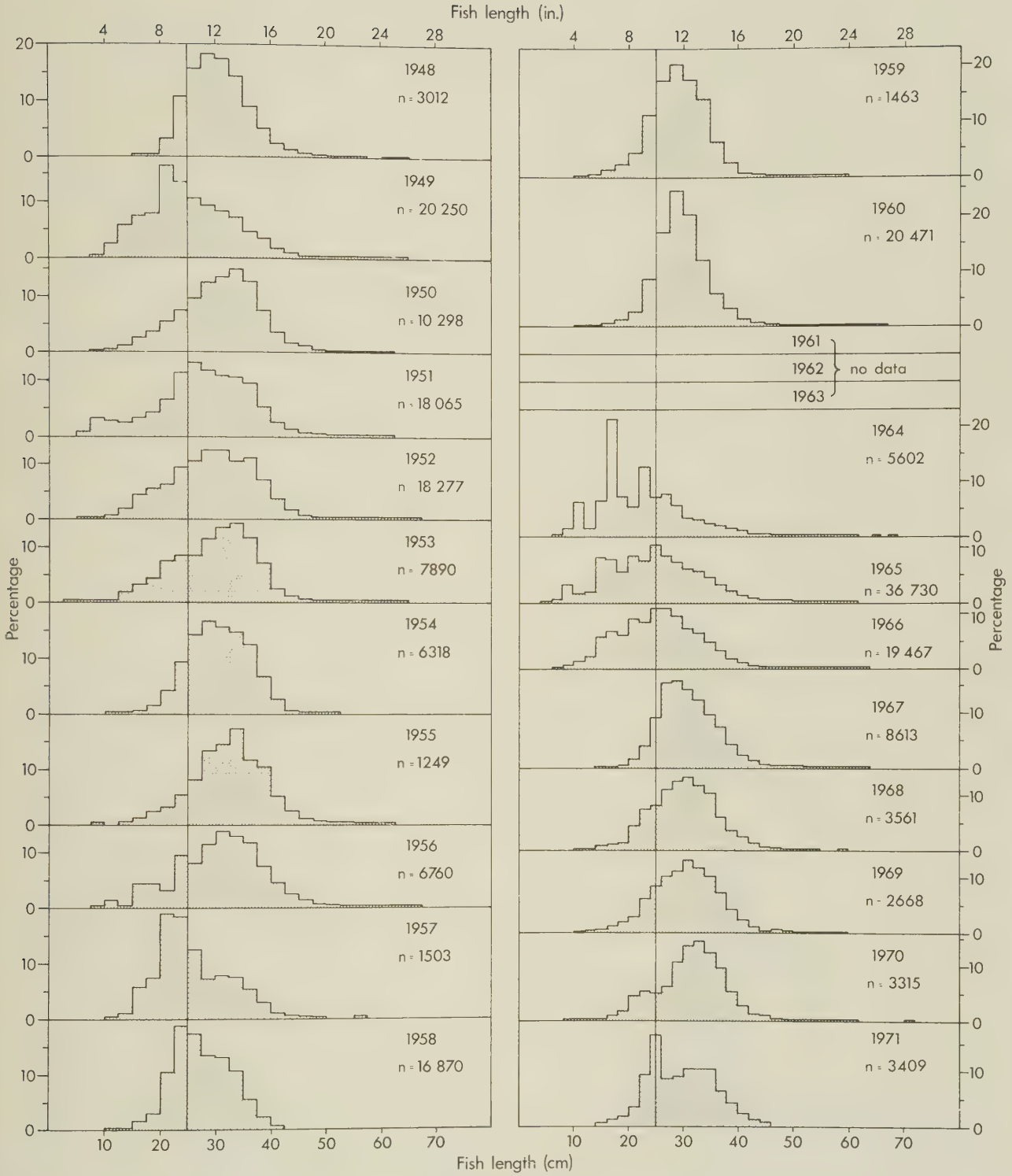

Fig. 28: Annual length-frequency distributions of trawl-caught snapper from the inner Hauraki Gulf, 1948–71. Several mesh sizes were used and several fishing grounds sampled; the greater number of small snapper in 1964–66 reflects the more extensive sampling on nursery grounds with a small-mesh net in those years. The vertical line is generalised at 25 cm, approximately equivalent to the legal size limit of 10 in.; it is also the 80% retention level with a 4-in. mesh. Measurements to 1963 are in half-inches and those from 1964 onwards are in centimetres; the original measurements have been grouped into inch and 2-cm units. For convenience the following approximations were adopted: 4, 8, 12, 16, and 20 in. equal 10, 20, 30, 40, and 50 cm respectively.

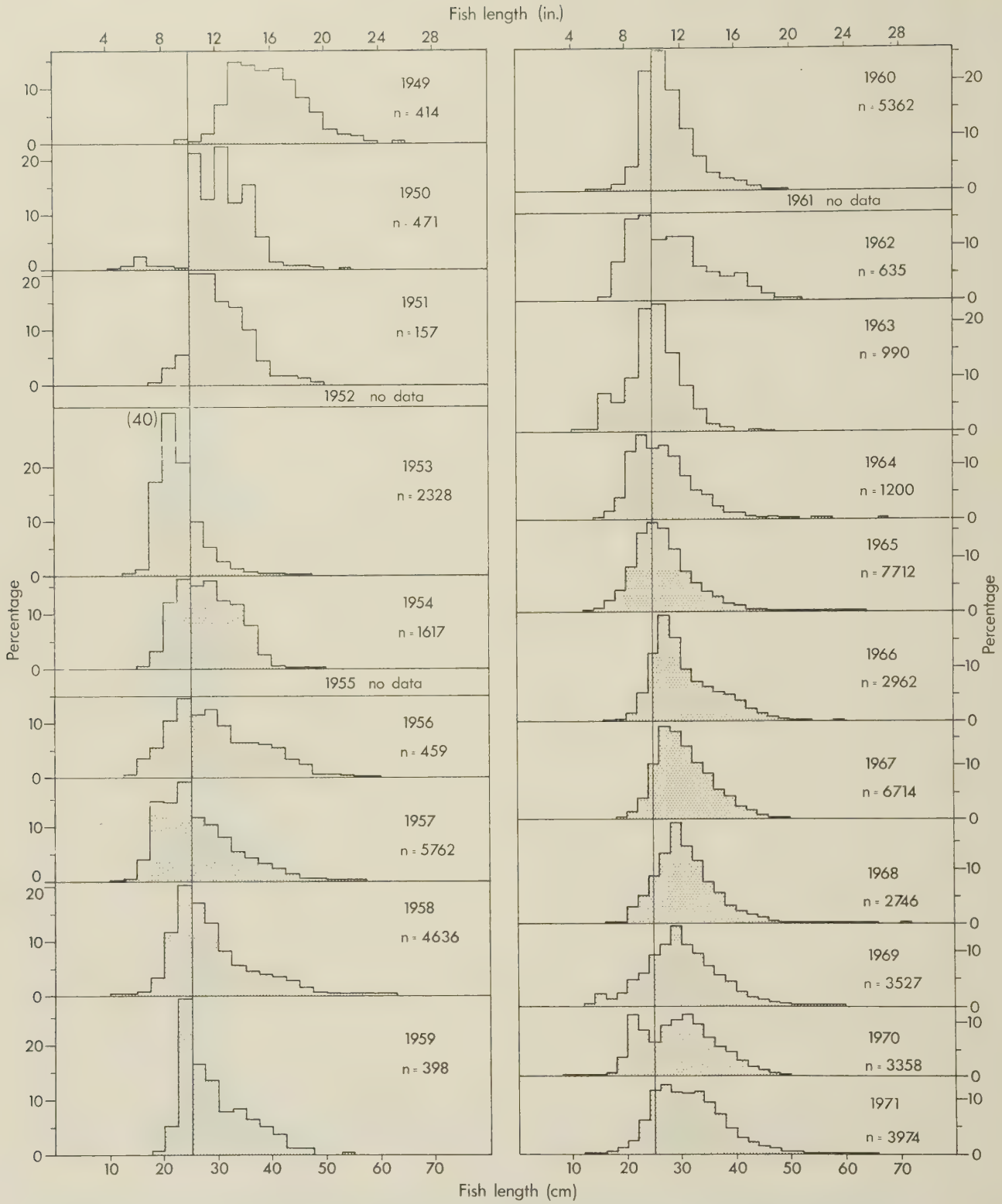

Fig. 29: Annual length-frequency distributions of trawl-caught snapper from the outer Hauraki Gulf, 1949–71. Several mesh sizes were used and several fishing grounds sampled. The vertical line is generalised at 25 cm, approximately equivalent to the legal size limit of 10 in.; it is also the 80% retention level with a 4-in. mesh. Measurements to 1963 are in half-inches and those from 1964 onwards are in centimetres; the original measurements have been grouped into inch and 2-cm units. For convenience the following approximations were adopted: 4, 8, 12, 16, and 20 in. equal 10, 20, 30, 40, and 50 cm respectively.

restricted to the actual catch of fish from which the sample was taken for ageing. In addition, because of inaccuracies of scale reading only fish up to 10+ can safely be assigned to year classes. Older fish, unless their otoliths have been read, must be grouped as 11 and older.

Length-frequency Distributions

The Fisheries Research Division has collected data on the size distribution of trawl-caught Hauraki Gulf snapper in most years since its research vessel *Ikatere* began working in 1948 (Figs. 28 and 29). The fish were caught during different research programmes, and the gear used included many mesh sizes, from a 12.7-cm (5-in.) single manila cod-end to a 2.5-cm (1-in.) synthetic cod-end liner. It would be impractical to try to apply corrections to each haul to reduce it to that which theoretically would have been taken by a net of standard mesh. It would also be unrealistic to consider only those samples taken by one particular mesh size, as this would eliminate many years' data whichever size was chosen. Consequently, the smaller sizes of fish are inconsistently represented in the histograms in Figs. 28 and 29.

Cassie's data on escape (1955, Fig. 34) show that 50% of 9½-in. (24.1-cm) snapper and 80% of 10-in. (25.4-cm) snapper are retained by a 4-in. (10.2-cm) mesh. The legal size limit for snapper is 10 in. (25.4 cm), and this is also the approximate size reached during the first significant spawning (see page 25). The vertical line at 10 in. (25.4 cm) in these and some subsequent figures thus separates juvenile, inadequately sampled snapper from adult fish, most of which would have been retained by the mesh size used. The vertical height of the histograms is naturally influenced by the proportion of small fish in the catch (hence by the mesh size), but the right-hand side of each histogram and the presence of modes above 25 cm are a good measure of the adult snapper caught.

The length-frequency distributions varied considerably from year to year. Some of the variations undoubtedly depended more on geographical differences in sampling intensity than on annual changes in population structure. The large number of juvenile snapper in the 1964–66 samples, for example, represented increased sampling on the in-shore nursery grounds during the early stages of the present study. Nevertheless, some interesting temporal trends became apparent even in this rather generalised presentation of data. The most obvious was an increase in the principal modal length from about 25 cm in 1964–65 to about 31 cm in 1971, apparent in both the inner and outer Gulf samples. This could have been caused by the slow growth of one or more dominant year classes produced in the early 1960s, a possibility examined in more detail below. The appearance of a new mode at 20–21 cm in 1970 indicates the appearance of a later abundant year class. Similar temporal shifts in modal lengths occur in other sections of these figures, which suggests the presence of earlier dominant year classes; for example, in the inner Gulf the movement of a mode past 25 cm in the late 1950s might represent an abundant year class spawned in the mid 1950s.

The right-hand sides of the histograms are similar to each other and also to the histogram of trawl-caught snapper measured by Hefford in the late 1920s (Fig. 27), which confirms Longhurst's observation (1958, page 492) that there has been no long-term change in the relative abundance in the catch of medium-sized and large fish. In most years there is a slight tendency for more larger snapper to be caught in the outer Gulf, the 1% level being reached at 50 cm compared with 45 cm in the inner Gulf.

The size range of snapper caught by Danish seine vessels in 1969–71 (Fig. 30) was broadly similar to

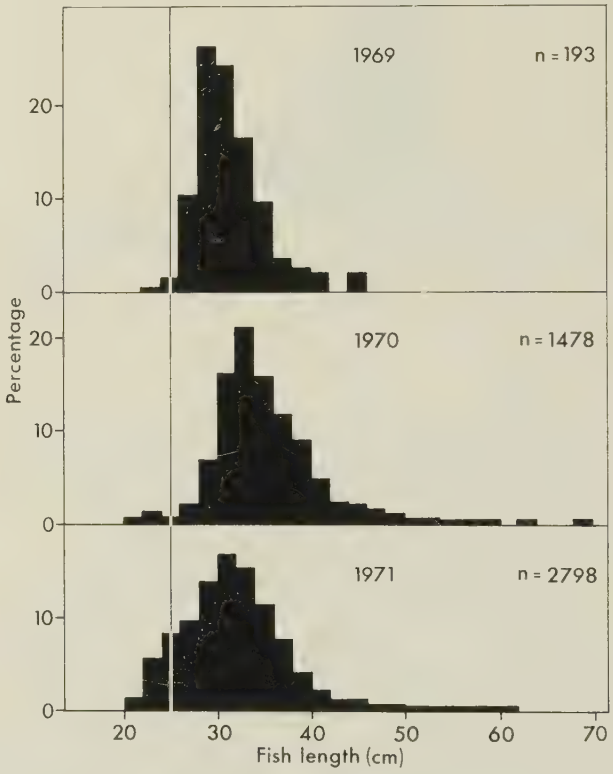

Fig. 30: Length-frequency distributions of Danish seine-caught snapper from the inner Hauraki Gulf, 1969–71. The 1969 sample was measured in a fish shed, and some of the smaller (under 25 cm) and larger (over 40 cm) fish may have been sorted out. The 1970 sample came from 8 catches, measured at sea, and the 1971 sample from 14 catches, measured at sea. The vertical line is generalised at 25 cm, approximately equivalent to the legal size limit of 10 in.

that of fish sampled by Hefford in 1927–29 (Fig. 27), with no significant change in average size.

No comparable recent samples have been obtained for snapper caught by long line or set net. These comprise only some 10–15% of total Gulf catches, and because they are landed in small quantities by about 200 small boats working 1- or 2-day trips out of numerous small harbours and bays around the Gulf, they could not be properly sampled during the present study.

Age-frequency Distributions

Trawl-caught Snapper. Although the high proportion of juveniles in the 1964 data (Fig. 28) is due largely to increased sampling on nursery grounds with a small-mesh cod-end liner, other samples measured in the Auckland fish sheds (Fig. 31), where considerable sorting and rejection of "under-sized" fish had already occurred, also show a dominant mode of small snapper at 26–27 cm (4-year-olds, the 1960 year class). This modal value was probably artificially high, many of the smaller 4-year-old fish being lost through escaping through the net and by rejection as under-sized by the fishermen. However, fish older than 10 years made up 35% of the sample by numbers and about 50% by weight, which showed that the trawl fishery—at least during early 1964—did not depend on a fairly small number of age groups, as might have been assumed from the length-frequency distribution alone.

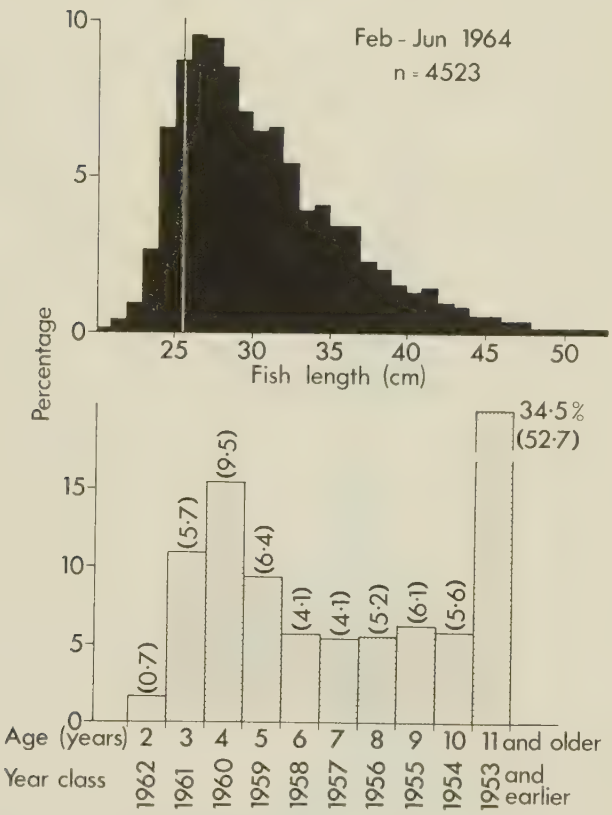

Fig. 31: Length-frequency and age-frequency distributions of trawl-caught snapper landed by commercial vessels from the Hauraki Gulf, February–June 1964. The "catch" comprises several fish shed samples, from which an unknown number of fish under 25 cm (10 in.) had been removed. The vertical line is at 25.4 cm, equivalent to the legal size limit of 10 in. The age-frequency distribution was calculated from the length-frequency distribution via an age-length key (700 fish aged by scale reading). The figures in parentheses are percentage weights, calculated from the age-length key and length-weight relationship.

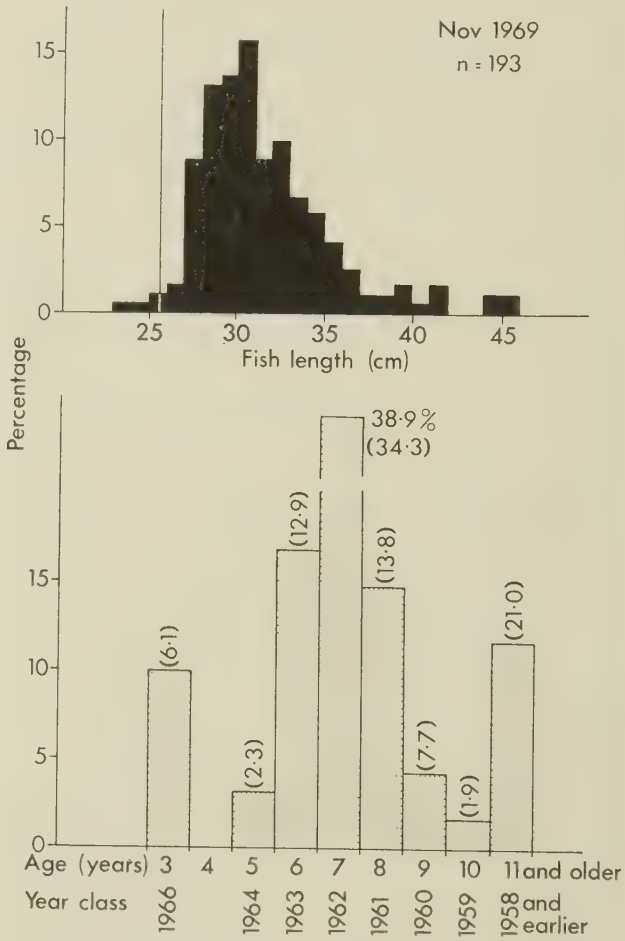

Fig. 32: Length-frequency and age-frequency distributions of Danish seine-caught snapper landed by a commercial vessel from the Hauraki Gulf, November 1969. The catch was measured in a fish shed, where some of the smaller (under 25 cm) and larger (over 40 cm) fish may have been sorted out. The vertical line is at 25.4 cm, equivalent to the legal size limit of 10 in. The age-frequency distribution was calculated from the length-frequency distribution via an age-length key (54 fish aged by scale reading). The figures in parentheses are percentage weights, calculated from the age-length key and length-weight relationship.

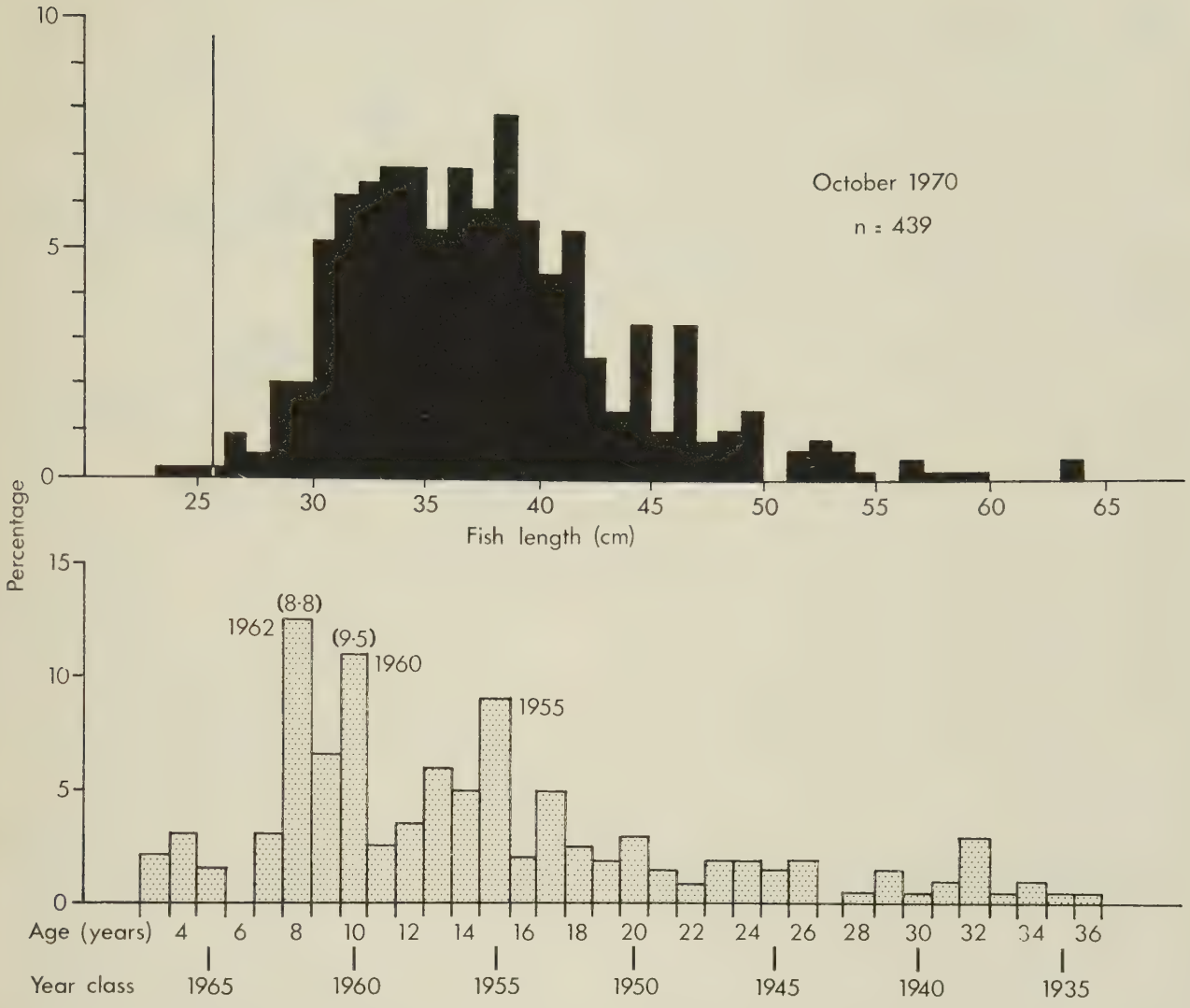

Fig. 33: Length-frequency and age-frequency distributions of a sample from one Danish seine snapper catch from The Noises islands area, Hauraki Gulf, October 1970. The sample is random from the catch. The vertical line is at 25.4 cm, equivalent to the legal size limit of 10 in. The age-frequency distribution was calculated from the length-frequency distribution via an age-length key (198 fish aged by otolith reading). The figures in parentheses are percentage weights, calculated from the age-length key and length-weight relationship. Fish older than 10 years comprise 60% by numbers and 73% by weight.

Unfortunately, the total length-frequency samples for trawl-caught fish from previous and subsequent years (Figs. 28 and 29) cannot be converted to age-frequency distributions via age-length keys, because the scale samples obtained do not cover the possibility that several stocks with differing growth rates and age compositions were sampled at different times throughout the year. It can only be postulated, from the essential similarity of the right-hand sides of most of the histograms in Figs. 28 and 29 to the upper histogram in Fig. 31, that fish older than 10 years generally predominated, with younger age groups, sometimes including dominant year classes, being numerically abundant but comprising less than half the weight of the catch.

Danish Seine-caught Snapper. Some data are available on the age composition of Danish seine snapper catches in 1969, 1970, and 1971 (Figs. 32–34). The size ranges of snapper in trawl and Danish seine catches were similar (see Figs. 28, 29, and 31), but Danish seiners caught fewer small (20–25 cm) fish, presumably because of their larger mesh size—12.7 cm (5 in.), compared with 11.4 cm ($4\frac{1}{2}$ in.).

The Danish seine samples were collected to examine a specific point: the size and age composition of the

large catches of snapper taken by this fishing method each spring and early summer (October to January). A popular belief among fishermen is that the fish which apparently school at this time of year belong to a distinct "race" of snapper which enters the Gulf from outside waters for spawning purposes only (Cassie 1956b). They are usually described by fishermen as being of uniform size, silvery with a bright reddish tinge, and with almost unworn teeth; fish of this description do certainly occur in many Danish seine catches and some trawl catches (personal observation). Longhurst (1958, page 492) suggested that they " . . . may not, in fact, be an aggregation of a relatively few year classes from the Gulf area to spawn, but may represent an onshore migration of a population . . . [from deeper water outside the Gulf]".

The 1969 sample (Fig. 32) did comprise a fairly small size range of fish, and though the sample size was small, the size range and modal size closely approximated those of the large sample of Danish seine fish measured by Hefford in 1927–29 (Fig. 27) and many of the trawl-caught samples in Figs. 28 and 29. The age-frequency distributions showed 7-year-old fish, the 1962 year class, to be dominant, being 39% by numbers and 34% by weight of the sample. Fish older than 10 years made up only 12% by numbers and 21% by weight.

The 1970 sample (Fig. 33) was completely different. There was a wide size range of fish, with a predominance of fairly large (over 35 cm) fish; such catches of so-called "large schoolers" are (according to fishermen) sometimes made during the season of peak snapper abundance. The age-frequency data showed a very wide range of ages, from 3 to 36 years. There were several clearly defined year classes. The 1962 and 1960 year classes were about equally abundant, each comprising about 11% by numbers and 9% by weight of the sample. There were several year classes spawned about the mid 1950s which were also abundant; the 1955 year class was nominally dominant in this group, but otolith reading is not sufficiently accurate at these ages (13–17 years) to guarantee the ages closer than ± 1 year. By the same division used before, fish older than 10 years made up 60% of the catch by numbers and 73% by weight, which was almost the reverse of the 1969 sample.

The 1971 samples were different again (Fig. 34). The size distribution of sample A was bimodal, with a small size group at 26 cm predominating. Scale reading showed this size group to be the 1968 year class, comprising 44% by numbers and 27% by

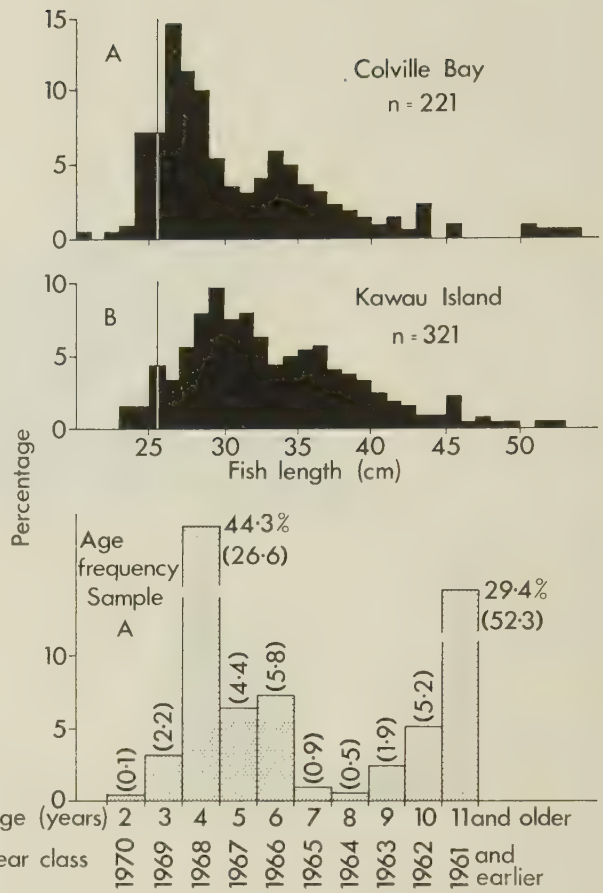

Fig. 34: Length-frequency distributions of snapper samples from two Danish seine catches (A and B) from the Hauraki Gulf, October 1971; samples are random from the catches. The vertical line is at 25.4 cm, equivalent to the legal size limit of 10 in. Age-frequency distribution of sample A (all 221 fish aged by otolith reading) is shown at bottom; the figures in parentheses are percentage weights, calculated from the age-length key and length-weight relationship.

weight of the sample. The age structure of the larger mode could not be determined by scale reading, because most fish 33 cm and larger were 11 years and older.

A second sample (B), from the same cruise but a different locality, was measured but not sampled for age. Although also bimodal, this sample differed considerably in the position of both modes, and it is probable that different year classes—perhaps including some which were poorly represented in sample A —were involved.

The results clearly show the variability of the commercial Danish seine catches and demonstrate that though dominant year classes do occur, their contribution by weight up to age 10 is generally overshadowed

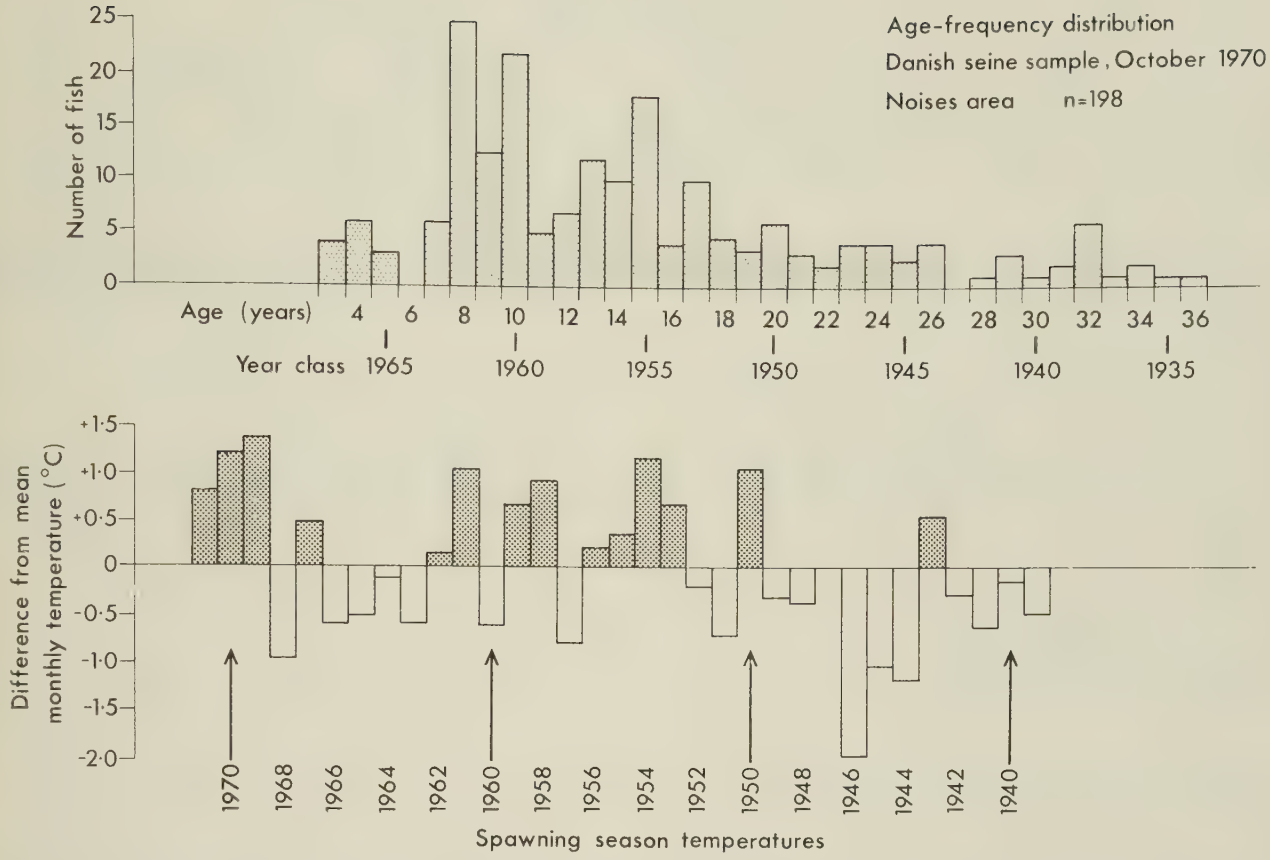

Fig. 35: Comparison between variations in year class strength of a 1970 Danish seine sample (from Fig. 33) and variations in climate (air temperature during spawning season). The temperatures are expressed as differences from the long-term mean monthly temperatures for November and December, Auckland City (New Zealand Meteorological Service 1930–72). The 1965 and younger year classes are not properly represented in the sample because of losses through the 12.7-cm (5-in.) seine net mesh.

by the high proportion of older fish in the catch. From the available data the year classes which appear to be dominant are 1968, 1962, and 1960, plus several from the mid 1950s.

Relationship between Year Class Strength and Spawning Season Temperatures

Water temperatures are sufficiently related to air temperatures in the Hauraki Gulf (Cassie 1956b, de Lisle 1965, Paul 1968b) for the latter to indicate annual variations in in-shore hydrological conditions.

In Fig. 35 the mean air temperatures in Auckland City for November and December (late spring, the peak spawning season) have been expressed as differences from the long-term mean for those months. The 1940s, with the exception of 1943, had cold springs. The 1950s generally had warm springs, particularly 1954, 1958, and 1959. The 1960s were variable, with very warm springs in 1961 and 1969 and cold springs in 1963–66 and 1968.

Also shown in Fig. 35 is the age-frequency distribution of the largest single sample of snapper (from Fig. 33) which was considered to be representative of the stock fished at least by seiners and to be reliably aged by otolith reading. It has been positioned in the figure to demonstrate the relationship between spawning season temperatures and the strength of the resulting year classes. There was good agreement between warm spawning seasons and strong year classes, in particular in the mid 1950s, spring 1959 and year class 1960, and spring 1961 and year class 1962. Because the sample was taken by a commercial vessel, the smaller fish (the 1965 and subsequent year classes) were under-represented, and their abundance cannot be compared with spawning temperatures.

The strong 1968 year class (Fig. 34) was spawned in the relatively warm 1967 spring. The cold springs from 1963 to 1966 produced relatively poor year classes (Fig. 34, and unpublished data from juvenile snapper surveys). The cold 1968 spring and warm

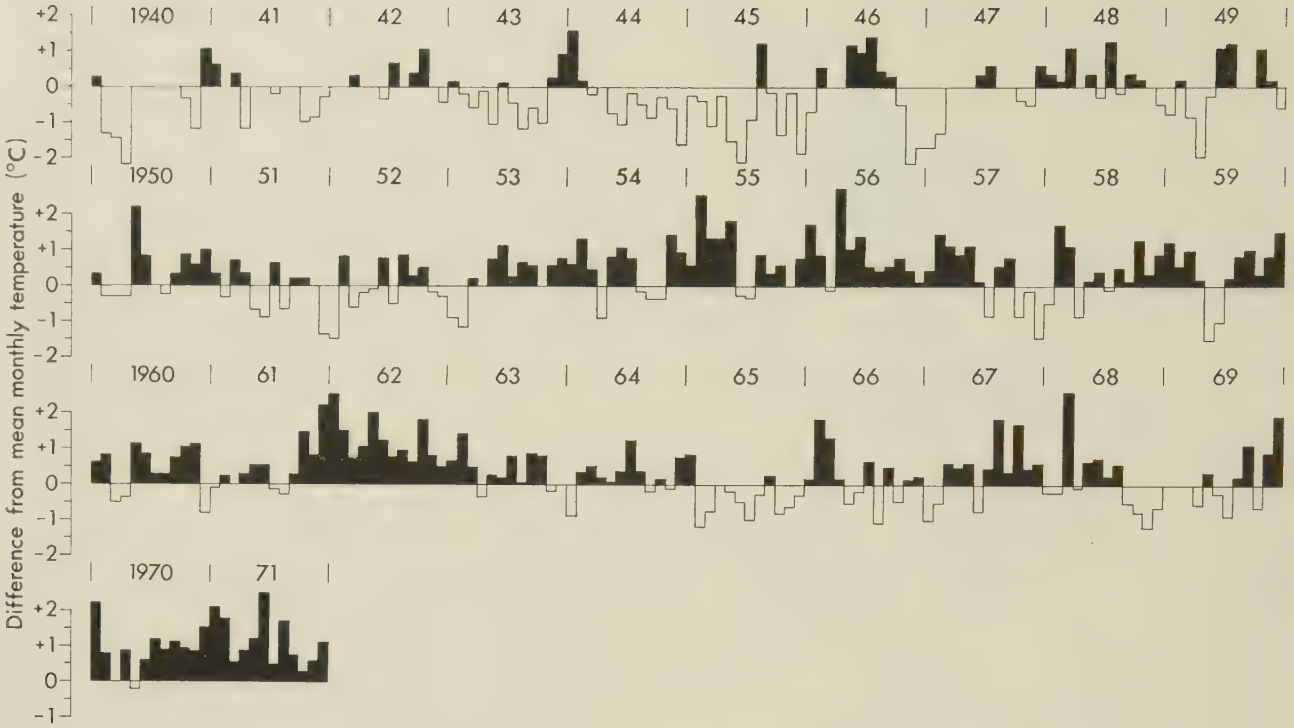

Fig. 36: Long-term variations in climate in the Auckland area expressed as monthly temperature variations from the long-term means from Auckland City, 1940–71.

1969 to 1971 springs appear to have produced poor and good year classes respectively (unpublished data).

It is unlikely that spawning season temperature alone influences year class strength. Temperatures during the first few months after spawning may also be critical; such temperatures for the strong year classes listed above were above average (Fig. 36).

DISCUSSION

The snapper occupies most marine habitats of the Hauraki Gulf, from deep water (150 m) near the shelf edge to rocky shore lines and shallow tidal inlets. It is long lived; 30- to 50-year-old fish are not uncommon. Despite a commercial fishery which takes about 3000 to 6000 tonnes annually, and an intensive but unmeasured sport fishery, snapper have remained common within the Hauraki Gulf. Much of the snapper's "success" must be its ability to exploit a wide range of habitats and take a wide variety of food organisms. Feeding studies (Powell 1937, Godfriaux 1969, 1970, Colman 1972) have shown the snapper to be a predatory carnivore, taking whatever food was locally most abundant and capable of being crushed in its strong jaws.

The growth rate of snapper is slow and variable. The variability may also be linked to feeding, as growth is fastest—for both juveniles and adults—in shallow areas, where water temperatures are warmest and the abundance and/or quality of prey organisms likely to be highest.

These variations in growth warrant further study, for apart from reflecting differences in feeding and environmental conditions, they might reveal the existence of more than one identifiable "stock" of snapper in the Hauraki Gulf area.

Variations in year class strength must influence the large commercial fishery for snapper on the Hauraki Gulf and adjacent grounds. This fishery, in its entirety worth several million dollars a year, is the mainstay of the Auckland industry.

Prediction of future yields will depend on an understanding of three factors: (1) short-term changes in fish behaviour, (2) longer-term changes in stock density resulting from overall fishing pressure, and (3) the effects of poor year classes.

There are two aspects to the question of variable year classes. Firstly, how significant are such variations? With a wide spread of age groups and a high proportion of older snapper in the fishable population the effects of two or three year class failures could be minimal. In such a contingency the state of older members of the population would be important in the maintenance of the fishery. Secondly, what causes year class variations? Is there any relationship with the size of the parent stock, or—as appears more likely—can variations be linked with environmental parameters? Temperature is the most obvious and easily measured, but its effects could be indirect. The apparent relationship between warm springs and strong year classes suggested by this study requires rigorous investigation. Variable features of the environment other than temperature must also be investigated.

The factors influencing year class strength will probably be related to some aspect of spawning and subsequent larval and early juvenile development. The general outline of snapper reproduction is known (Cassie 1956a, 1956b, 1957a, 1960), but information on optimal conditions for gonad maturation, spawning behaviour, egg survival, hatching, and larval development and the subsequent survival of larvae and early juveniles is lacking. At some future time the snapper may be considered for marine fish farming in warm shallow bays in northern New Zealand (being similar to the red sea bream *Chrysophrys major*, already successfully farmed in Japan), when information on its early life history will become especially important.

Studies on the relationship between population age structures and commercial fishing success will depend on identification of year classes in regular samples of fish taken from the commercial catch or landings by all major fishing methods. Age determination by scale and otolith reading, as outlined in this bulletin, should provide adequate results, but there are aspects of both methods which require clarification before older fish can be aged with precision. In particular, the cycle of ring formation in otoliths should be closely examined; recent work on other species of fish (for example, Reay 1972) shows that this topic is complex and controversial and has considerable implications for precise age and growth work.

One of the most important unresolved problems in snapper research is the question of how many "stocks" or "populations" of snapper inhabit the Hauraki Gulf. They are not separable by morphological or meristic features (Cassie 1956b, page 310, J. A. Colman pers. comm.), but they might be identifiable from differences in age composition or, as noted above, growth rate. The phenomenon of "school snapper"—the presence of large concentrations of apparently schooling fish in certain parts of the Hauraki Gulf during the spring and early summer spawning season—must be examined in this context. Are they resident Gulf fish which adopt a brighter coloration and different patterns of behaviour during the spawning period? Or are they snapper which migrate into the Gulf only for spawning purposes and

comprise a separate "stock" of fish normally resident elsewhere? Large areas of rough, untrawlable, and somewhat unexplored sea bed exist north and northwest of the Hauraki Gulf, from Great Barrier Island to Cape Brett, which, lying in the warm East Northland Current, would theoretically provide an ideal habitat for snapper. These possibilities are not mutually exclusive. "School snapper" may comprise fish from the Hauraki Gulf, as well as from grounds outside the Gulf, the latter group entering the Gulf only in spring in search of a suitable spawning area.

The significance of the possibility that more than one stock of snapper can be fished within the Hauraki Gulf is that measurements of natural and fishing mortality, reactions to fishing pressure, and the like become complicated. For example, a resident Gulf stock may become severely overfished while an immigrant spawning stock remains only lightly fished; subsequent management procedures would need to recognise this. The existence of a separate "spawning stock" would also have to be taken into account in studies on spawning and variations in year class strength.

"School snapper" are sought by fishermen because of their abundance and their good, fat condition. Other groups of snapper, however, cause problems by their abundance. Fish in their third and fourth years of life are slightly smaller than the legal size limit of 10 in. (25.4 cm), but occur in considerable numbers on some of the main trawling and seining grounds, particularly when the year classes involved are strong ones. Many are taken in trawl and seine nets and are dead when returned to the water. The 10-in. size limit was set arbitrarily as a convenient size for measurement and so the problem is not simply that of determining the correct mesh size for the proper escape of these "under-sized" fish. The first requirement is to determine the correct size at which snapper should be exploited. Moreover the small snapper problem cannot be resolved by excluding seiners and/or trawlers from nursery grounds, because the distribution of these smaller fish is widespread and variable and overlaps the distribution of larger fish. The seasonal movements of these fish include an in-shore/off-shore component, but they are not well understood.

This study, in common with most studies of commercially exploited marine species, was oriented towards understanding some of those aspects of the snapper's biology which are important to the rational management of its dependent fishery. The work has shown that the species is common and long lived and that many features of its life history are variable.

SUMMARY

The snapper, *Chrysophrys auratus* (Forster, 1801) (family Sparidae), is most common in northern New Zealand coastal waters, where it is a major component of commercial trawl catches. The Hauraki Gulf is the most important snapper fishing ground, and Auckland is the major port for catch landings.

This study was directed towards obtaining more reliable information on the growth rate of snapper, the age composition of the Hauraki Gulf snapper stock, and some understanding of biological factors responsible for the fluctuating landings at Auckland.

Material was obtained from a small research trawler and commercial trawl and Danish seine catches.

Growth rate was determined by length-frequency analysis, scale reading, and otolith reading.

Length-frequency analysis showed mean lengths at the end of each of the first 4 years of life to be 11, 16, 20, and 24–25 cm respectively. Most growth occurred during summer and early autumn. Scale annuli in juvenile fish were clear and could be easily counted. They formed during winter and became visible when growth resumed in the following spring. The annuli of adult fish became visible a few months later, in summer or autumn. Scales with more than 10 annuli were difficult to read because of close crowding of annuli at the scale edge.

A nomograph was developed to facilitate back calculating fish growth from scale reading measurements.

Otoliths, read from a polished and burnt cross section, agreed with scale reading and length-frequency interpretations of age, though otoliths from fish older than 10 years usually had more rings than there were annuli on the scales, which suggests that somatic growth (as represented by scale growth) could decline or cease in later years.

Some variation in growth was found in juveniles and adults. Faster growth occurred in shallow, sheltered water, and there was some indication of more than one "population" or "stock" occurring. The growth rate determined during this study was considerably slower than that described by earlier workers. The increase of weight with length and age is described.

Small juveniles inhabited shallow bays and harbours, and larger juveniles were found in progressively deeper water. There was an off-shore movement in winter which became more distinct with the attainment of sexual maturity.

The distribution and migration of adult fish were complex. More than one "population" or "stock" of snapper may have been present during the sampling period.

The age composition of the commercially exploited "stock" varied annually. In most years the majority of fish, and the bulk by weight, were more than 10 years old. In 1971 the strong 1968 year class appeared in the peak seasonal landings by Danish seiners. Other strong year classes were detected in Danish seine catches of "schooling snapper"; these included the 1962 and 1960 year classes and one or more from the mid 1950s. These strong year classes were spawned during warmer-than-average springs. Variations in year class strength are one factor influencing the commercial landings at Auckland.

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